# Culture and Larval Behavior of Photurid Fireflies

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ABSTRACT: Techniques are presented for collecting firefly larvae and for laboratory cultures providing adults in any month of the year. Temperatures below about 16 C prevent pupation, and constant darkness causes 90% inhibition of pupation and delays the adult eclosions that do occur. Larval body-weight frequency distributions for nine field samples, plus laboratory and field observations, suggest a 2-year life cycle for the species studied. Some aspects of larval behavior are discussed in relation to light emission.

## INTRODUCTION

Study of the physiology and behavior of American lampyrid fireflies is severely restricted by the fact that live adults are available during only a few weeks in summer. Laboratory culture of two Asian fireflies having aquatic larval stages has been successful (Kiichiro, 1961; Katsuno, 1963; Haneda *et al.*, 1964), but no practicable method for rearing other lampyrids has been developed.

Experiments in this laboratory over the past 10 years have led to procedures for obtaining adult fireflies of the genus *Photuris* in virtually any month of the year. In addition, our experience with the habits of larvae in field and laboratory fills some gaps in present knowledge of lampyrid behavior and life history.

Since our procedure for obtaining adult fireflies at particular times starts with full-grown larvae, the work has been limited to larvae of *Photuris*, the only local variety obtainable in adequate numbers. (It is noteworthy that larvae of the most abundant firefly in the region, *Photinus pyralis*, are practically never found above ground.) The larvae could not be identified to species but almost all the adults that emerged belonged to Barber's (1951) *P. versicolor* and *P. lucicrescens* (Figs. 13-18).

*Habits and distribution.*—The general appearance of *Photuris* larvae is shown in Figures 2-6. During the day the larvae presumably live in the soil. At night they appear on the surface, crawling among grass and weeds and sometimes climbing up a few inches on stems, particularly if the weather is damp. Our best collections were made from thick but relatively short grass such as occurs on golf courses (which are favorable also because of relative freedom from distracting house and vehicular lights). In such an area there may be up to 10 larvae per sq yard, and an experienced hand may collect up to 300 in an hour. Few larvae were found on ground exposed to full sunlight for long periods, except in swampy regions. Rather, they were most

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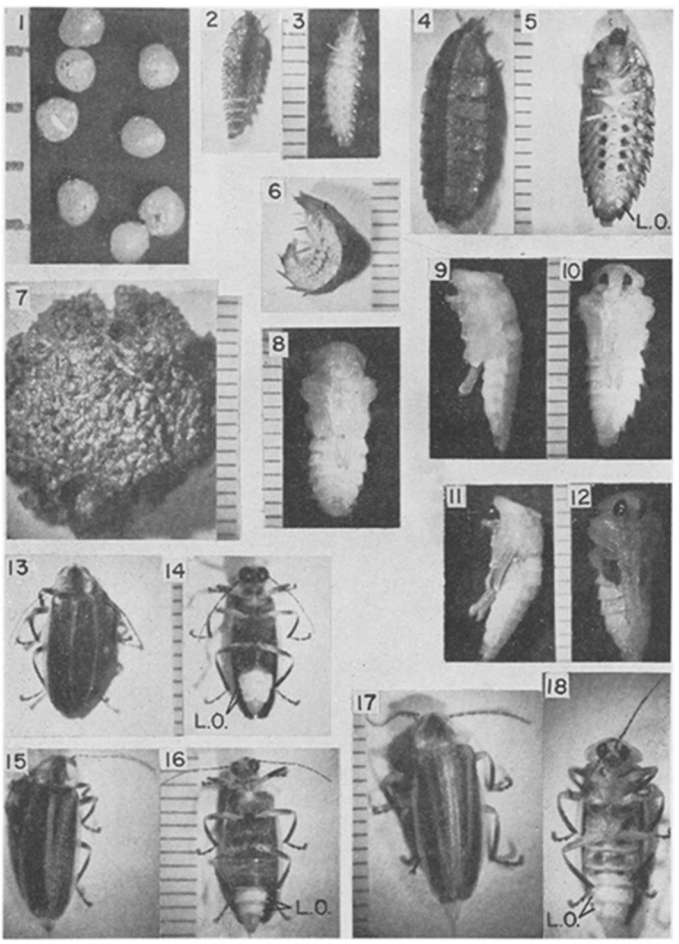
abundant in well-shaded areas such as forest margins, low-lying copses and the banks of ponds and streams. They were not common in thick forest or open fields. It seems clear that moderate ground temperature and high microenvironmental humidity are essential for life, as is suggested also by the fact that larvae shrivel up and die in a few hours if left in a dry container at room temperature. Larvae are more abundant and active on foggy or drizzly nights than on dry ones, and




Figs. 1-18.—Stages in *Photuris* development. (For all figures: scale divisions in mm. L.O. = light organ.) 1.—Eggs. 2, 3.—Dorsal and ventral views of fourth-stage larva 1 day before ecdysis. 4, 5, 6.—Dorsal, ventral and lateral views of mature larva. 7.—Pupation cell (removed from soil and sprayed with lacquer). 8.—Ventral view of 1-day-old pupa. 9, 10.—Lateral and ventral views of 7-day pupa. 11, 12.—Lateral and ventral views of 9-day pupa. 13, 14.—Dorsal and ventral views of adult *P. versicolor* male. 15, 16.—Dorsal and ventral views of adult *P. versicolor* female. 17, 18.—Dorsal and ventral views of adult *P. lucicrescens* female

on warm nights than on cool. They are usually found higher up in the grass the damper the conditions. Some local areas from which larvae have been collected regularly are known to have been submerged for several hours during flash floods. Ambient and extraneous light impedes collecting by causing reflections from leaves, by reducing the relative visibility of the larval light and by actual inhibition of luminescence. Even moonlight has an inhibitory effect.

Larvae are collected at night, being first located by their light and then sifted out from the grass. On favorable dark nights (temperature 15 C or above, with heavy dew or after a rain), with the larvae well up in the grass, the bright green glow of a single individual may be visible for 50 ft and may persist for several seconds. Since the larvae usually keep their lights on during handling, and since it is desirable to maintain visual dark-adaptation, it is preferable to make the capture by touch rather than to use a flashlight. With a little practice the fingers become adept at identifying the larval body, even deep in the grass.

In the Washington area, large larvae are available in April and May, after the start of the warm spring rains, but are practically unobtainable during June and July, when the adults are abundant. Some medium-sized larvae can be found in August if the weather is not too hot and dry, but the best collecting period is from mid-September to mid-October, when the heavy dews and drizzles of autumn have begun and before fallen leaves blanket the ground. In mild years a few larvae have been found into November.

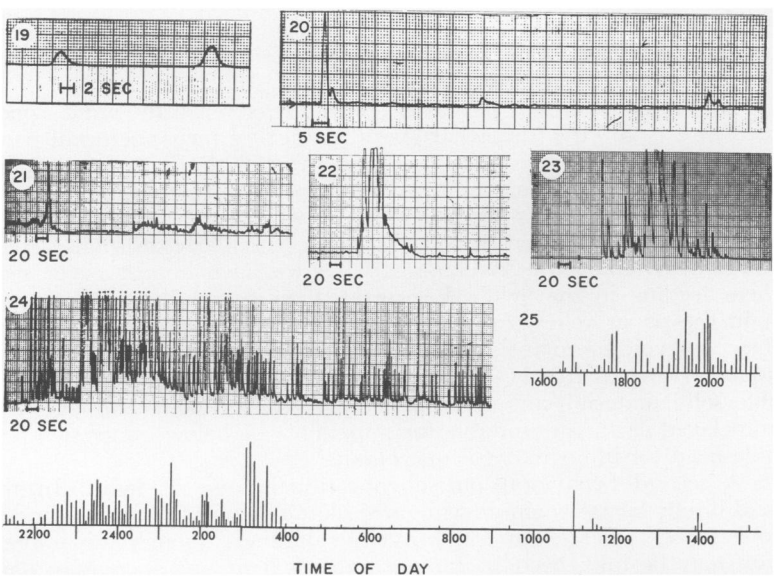
*Larval behavior.*—Even after collecting several thousand specimens, we have little idea what larvae do during their nocturnal peregrinations. On both bare ground and in grass they seem to wander aimlessly, hitching along the tip of the abdomen rhythmically like an inchworm, and turning on their lights periodically. Though firefly larvae have been shown to be predatory, particularly on snails (Hess, 1920; Schwalb, 1961; Williams, 1917), we have almost never seen them feeding in the field. Larvae kept on damp filter paper often stain the paper yellow for some days after collection, suggesting that they are voiding plant pigment. Microscopic examination of gut liquid of several freshly collected larvae did not reveal any recognizable solid material, animal or vegetable. Experiments showing that autoclaved earth is unsuitable for pupation (*see* below) suggest a possible need for interstitial soil microfauna.

A second behavioral puzzle concerns the use of light. In the field, firefly larvae begin glowing at dusk. The number active appears to increase thereafter at least until full darkness, though this impression may be influenced by fading ambient light and increasing dark adaptation of the observer. Activity in the field has not been followed later than midnight, but captive larvae continue to locomote and glow periodically until dawn. Two kinds of emission have been noted. The first is a moderately bright glow lasting 1-3 sec and recurring during locomotion at more or less regular intervals of 10 to 60 sec. The laboratory record shown in Figure 20 may represent this type of emission. The second is a very bright single glow that lasts 5 or even 10 sec and recurs, if at all, only after several minutes (Fig. 21, near

start). This type of glow appears to be emitted while the larva is at rest. Other types of luminescence recorded under artificial conditions, which are described later, may be exaggerations of field behavior.

The possibility of light being used by the larva to find its way about seems remote in view of the animal's minute eyes and the tangle of vegetation in which it habitually moves. Communication is equally questionable. Larvae kept together in a container certainly appear to light up more frequently than larvae in isolation, but this can well be due to mechanical disturbances as they crawl over one another. In the field it sometimes seems that larvae light in groups — that is, if a larva in a given area lights, two or three others may soon glow in the immediate vicinity. But even if such groupings were statistically valid, they might simply represent larvae derived from the same batch of eggs or attracted by food rather than indicating use of light emission in assembly or signaling. Tests with several larvae in separate 5-cm petri dishes set close together indoors at night gave no convincing evidence that glowing by one individual stimulated luminescence by another.

*Characteristics of light emission.*—As described and illustrated by numerous workers (*e.g.,* Williams, 1916; Hess, 1920), the larval light




Figs. 19-25.—Spontaneous light emissions of mature *Photuris* larvae with time. Intensity (vertical deflection) arbitrary. Each record from a different larva. 19.—Fast recording to show contour of single glows. 20.—Glows at intervals of 50 to 70 sec. 21.—Sustained repetitive glowing, sometimes superimposed on continuous luminescence. 22.—Concentrated burst of luminescence. 23.—Same, with total darkness preceding and following. 24.—Sustained high intensity glowing at relatively high frequency. 25 (continued below).—Diagram of 24-hr light emission pattern showing virtual absence of glowing between 4 AM and 5 PM

organs consist of a pair of small oval spots on the ventral surface of the last abdominal segment (Figs. 3, 5, 6). Light emission was recorded from individual larvae in a totally dark cylindrical duraluminum chamber 30 mm in diam and 20 mm deep, with a transparent plastic top. The chamber walls were lined with wet filter paper and the chamber was attached to the housing of an RCA 1P21 photomultiplier tube feeding into a chart recorder. Because of reflection from the filter paper, the light emitted was easily visible from above when the larva was in the normal dorsum-up position. Since larvae were free to move in the photometer chamber, some changes in apparent light intensity could have been due to different degrees of exposure of the (ventral) light organs. However, the larvae move slowly and strongly prefer to keep their dorsal surfaces up, so movement was unimportant insofar as the rapid transients in the records are concerned.

As shown by Chang (1956), Buck and Case (1961) and Carlson (1965), the basic single larval glow is a nearly symmetrical emission lasting 1 to 3 sec (Fig. 19). Even in our artificial but stable conditions the glows varied greatly in timing and intensity. Some larvae tended to give short, sudden bursts of glowing amid long periods of quiescence (Figs. 19, 20, 22, 23) while others produced an almost incessant series of closely spaced glows for long periods, sometimes superimposed on low-level continuous emission (Figs. 21, 24).

Seven larvae were monitored continuously for periods of up to 80 hr. Two failed to emit any light over many hours even though they had been crawling actively (as indicated by the shredded filter paper) and were presumably capable of glowing, since they lit up upon mechanical stimulation after removal from the chamber. The other larvae all showed prolonged periods of bright, spontaneous glowing, usually very irregular, and sometimes interspersed with long periods of virtual inactivity. Usually the periods of luminescence did not correspond either in real time or length to true day and night, but one larva showed diurnal periodicity consistently corresponding with actual day length and almost totally confined to actual dark hours (Fig. 25). This periodicity continued for nearly 72 hr, the duration of the experiment, with the pattern beginning to degenerate during the 3rd 24-hr period.

One further finding in the photometer experiments was a response to mechanical vibration shown by some larvae after long periods without light emission. Very delicate contact with the external surface of the chamber was sufficient to trigger an extremely bright burst of light. Three or four such paroxysms, decreasing in intensity, could be induced by stimuli a few minutes apart before the larva became refractory. The existence of such hypersensitivity points to the need for careful shock-mounting of photometric equipment used to study spontaneous luminescence.

*Larval storage.*—As already implied, the most efficient method for obtaining adult *Photuris* fireflies out of season is to collect mature larvae, hold them until a particular time before the adults are needed, then induce them to pupate and complete their adult development.

Firefly larvae have an impressive tolerance of inanition and may

live unfed for many months at 10 C. Water is the most critical requirement: even large larvae cannot endure dry conditions for more than an hour or two and small larvae shrivel in minutes. In addition to the need for high humidity, drinking water, such as that held in saturated filter paper, must be available. We routinely store larvae in groups of 30 in 15-cm petri dishes floored with two sheets of wet filter paper, checking the moisture weekly, changing the soiled paper and washing the larvae about every 3 weeks.

Storage temperature is not critical. Larvae survive even at 5 C for long periods, requiring less attention than at intermediate temperatures but having also a somewhat greater mortality and lower potential for adult development. Larvae at room temperature also live well for extended periods (over a year in a few instances) but require more feeding than at intermediate temperatures (*see* below), have a higher mortality and are more susceptible to fungal, mite and viral infection. On the whole we consider 10 C the most convenient holding temperature.

Though mature autumn larvae can sometimes complete development without additional feeding, we routinely offer food, particularly for the first few weeks after collection and when pupation is being induced. Chopped horsemeat and moistened cat food pellets (Little Friskies, Carnation Co.) have been the most commonly used foods, the latter being the most convenient, but nutritional requirements have not been studied systematically. Larvae will also eat small live earthworms and snails, chopped insects, Tubifex worms, beef, liver, creamed cheese, boiled egg yolk, some vegetables and gelatin. They also scavenge dead dishmates and may cannibalize sick or newly molted companions or even pupae and newly emerged adults. Feeding is promoted by temperatures of 20 - 25 C and by darkness. The uneaten food and soiled paper should be removed within 24 hr. Large larvae at room temperature are fed at 2-3-week intervals, cold-stored larvae at 4-6-week intervals and small larvae more frequently (*see* section on development).

*Induction of pupation.*—In nature, the pupation of *Photuris* larvae, taking place in May and June in Maryland, involves the construction of a chamber or igloo of small pellets of soil, partly under the surface of the ground (Fig. 7; *cf. also* Hess, 1920). In this cell the larva sheds the last larval skin, pupates and undergoes adult development (Figs. 4, 5, 8-12). Large larvae collected in May sometimes pupate almost immediately, but those obtained in the autumn require at least 50 days, and more commonly close to 100, to yield mature fireflies. Much of the delay is involved in reaching the stage of cell building, but sometimes the larva will build a cell and lie in it for some time before pupating. The actual building of the pupation chamber takes only a night or two while pupal and adult development occupies about 15-20 days at room temperature. The delay in metamorphosis of autumn larvae means, incidentally, that fireflies needed between August and mid-November must be derived either from 9- to 12-month-old larvae (in which eclosion percentage is reduced; *see* below) or from large spring larvae held at reduced temperature until a month before adults are wanted.

Apparently the presence of natural soil is very important to pupation, for although we have had a few animals that either managed to construct a satisfactory chamber out of pulped paper or peat moss or even to pupate without any chamber, this is exceedingly rare. Autoclaved earth is completely unacceptable. To induce eclosion we put the larvae in a closed container on 1 to 2 inches of moistened sifted loam from a firefly habitat and kept them at 23 to 27 C in a cabinet maintaining 80-90% relative humidity. Methacrylate refrigerator boxes 9 x 12 x 18 cm serve well for 30 larvae.

We have not detected any marked change in larval appearance signalling a prepupal stage, but readiness for pupation appears to be greater the larger the larva of a given postcollection age. As storage time passes, there also tends to be an increase in the behavioral signs of readiness for pupation, such as paper-chewing, attempts at igloo-building, disinterest in food and sluggishness. The passage of time seems to be more important in development than the attainment of some limiting size. Thus, from smallish larvae 10 months after collection it is possible to obtain adult fireflies less than half the weight of those derived from large larvae pupating in autumn. On this basis all larvae longer than 10 mm and heavier than 60 mg can be considered potentially "mature." Extra-large larvae seem to produce female adults more often than males.

The pooled eclosion times for adults derived from 570 autumn larvae after a variety of periods at low temperatures, mostly in the dark, are given in Figure 26. The average development time for individuals that built and pupated immediately after being put on soil is believed to be approx 20 days, the later eclosions being due to delays

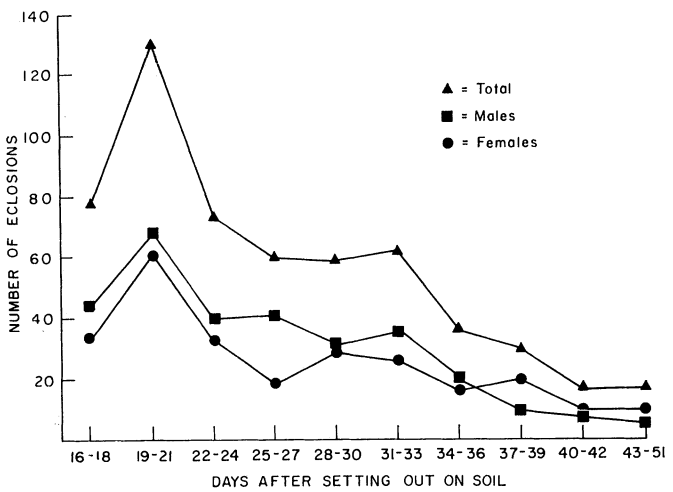



Fig. 26.—Numbers of *Photuris* eclosions at various times after being placed on dirt at room temperature. Cumulative record of 570 autumn-collected larvae, 1964-68, all of which were cold-stored for at least 60 days before setting out for pupation on day 0. Points joined by lines to make grouping separation clearer

in cell building and pupation rather than extension of the actual time of adult development.

*Effects of light and temperature in induction of pupation.*—At any time of year *Photuris* larvae exposed to room temperature, even after many weeks in the cold, recover quickly from their torpidity. This indicates that no diapause is involved. Nonetheless, our earlier work on autumnal collections had indicated that for most larvae a 6- to 8-week period at low temperature was necessary before pupation could be induced. Recently, Dr. Katherine Smalley (pers. comm.) obtained evidence that a 16/8 hr light/dark cycle makes temperature conditioning unnecessary in *P. divisa* and *P. missouriensis*. In order to clarify the effects of light and temperature on development of local *Photuris* the following experiment was performed.

A total of 216 larvae from one locality, averaging 82 mg (range 70-150), were kept unfed on damp filter paper at room temperature and normal October photoperiod for 20 days after capture. They were then distributed equally into four opaque and four transparent refrigeration boxes prepared with moist loam as already described. One opaque and one transparent box were stored in an environmental chamber at 25 C and 80-85% relative humidity, the other six at 7 C and 65-80% relative humidity except for biweekly defrost periods of about an hour. Both warm and cold chambers were programmed for a 16-hr light/8-hr dark regimen, the light coming from six 15 w lamps at an average distance of 50 cm from the containers. Pairs of boxes (clear plus opaque) were transferred from the cold to the warm chamber at the end of 20, 40 and 60 days. Clear boxes were examined for newly hatched fireflies each morning; dark boxes were checked every week or two in deep red light.

Of the animals exposed to a light/dark cycle, an average of 82% metamorphosed, with a 1:1 sex ratio. Exposure to low temperatures was not necessary to induce eclosion (Fig. 27, Box I). Cold storage delayed eclosions by slightly less than the amount of time in storage. These data indicate that development is inhibited at low temperatures. Further experiments indicated that eclosions do not occur below 16 C. However, some changes must be possible during exposure to low temperatures since less time is required for eclosion after returning animals to the warm chamber (30 days median for Box VII vs. 41 days for Box I in Fig. 27).

Only 12 of the 108 animals reared in darkness metamorphosed, six of them in the box stored 60 days at 7 C before transfer to 25 C. There was no apparent difference in the average eclosion times for the four opaque boxes (94, 102, 96 and 110 days).

*Maintenance and breeding of adults.*—In laboratory cultures adults normally eclose at night. With a uniform batch of larvae all the adults in a rearing box may emerge in 3 or 4 days, but often a month may elapse between the earliest and latest. Batch yields have ranged from 50-95% of the starting larvae, the percentage falling with storage age.

Adults can be kept alive in individual, loosely capped vials with a strip of wet filter paper for 15-20 days at 23-27 C and for as long as 30 days at 5-15 C. Adults of both sexes will drink sugar water from filter paper, but it is uncertain whether life is prolonged by such feed-

ing. In nature the *Photuris* female is well known for predation on other species of firefly and for cannibalism (Williams, 1917; Barber, 1951; McDermott, 1958, 1964; Lloyd, 1965).

Field-collected *Photuris* females will often lay fertile eggs in the storage vial. Laboratory-raised females will mate and lay, and a covered and humidified glass cylinder 50 x 25 cm is a satisfactory chamber. The eggs are easier to find if the females, after several days in the mating enclosure, are put individually in loose-capped 4-oz jars in a warm, humid environment in dim light. Damp peat moss, loam or crumpled damp filter paper can serve as media for egg deposition, with soil apparently preferred but in which the eggs are harder to find. Eggs are laid over a span of 1-4 days, the number varying from a few to about 100. Eggs are usually found in groups of 3-7, slightly below the surface (Fig. 1), but when space is limited or filter paper used they are apt to be in a mass. Virgin females will eventually lay also, though those eggs never hatch.

*Development.*—Eggs must be kept at 100% relative humidity. At

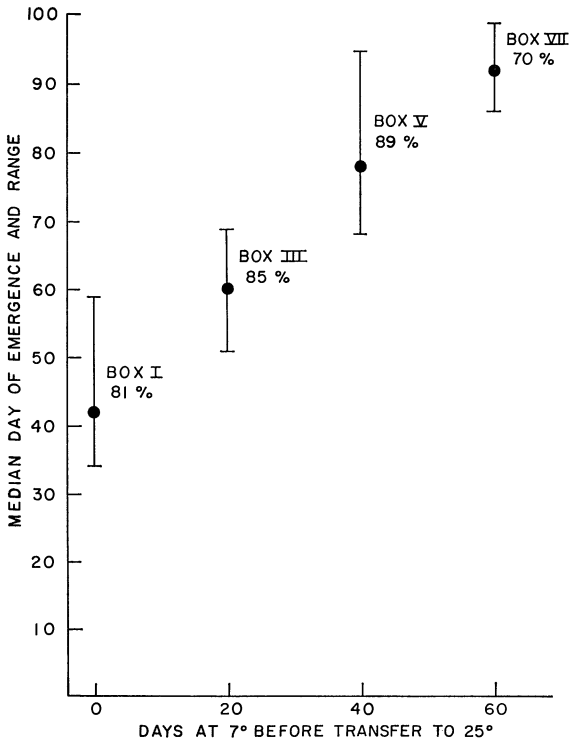



Fig. 27.—Effect of sojourn at 7 C on eclosion times of light-exposed larvae after transfer to 25 C (*see* text). Solid circles represent the median number of days before eclosion and the range is given by the vertical bars. Percentages are the proportional eclosions in the respective groups. The difference in time scales in Figs. 26 and 27 is because Fig. 26 includes many larvae that had cold exposures of several months and hence were more disposed to quick pupation

25 C development requires about 14 days (*cf.* Williams, 1916). Hatchlings are 2-mm miniatures of the mature larva except for being unpigmented. By the day after hatching they attain their typical yellow-brown to dark grey-brown color. A similar melanization occurs after each molt. The larvae may be fed on moistened cat food pellets a day or two after hatching and thereafter two or three times a week for several weeks.

At 25 C we found the first four ecdyses to occur on the average at 18, 35, 45-60 and 85-100 days after hatching, respectively. Disparities in size increased after the second molt (*cf.* Williams, 1917). Mortality has been about 50% in the first instar, 15 to 25% more in the second, and by the time the third molt has taken place only 10-30% of the original brood is left. Survival of laboratory-hatched larvae past the fourth instar has been rare, though some have lived and grown for over a year. Only a single animal was actually carried all the way

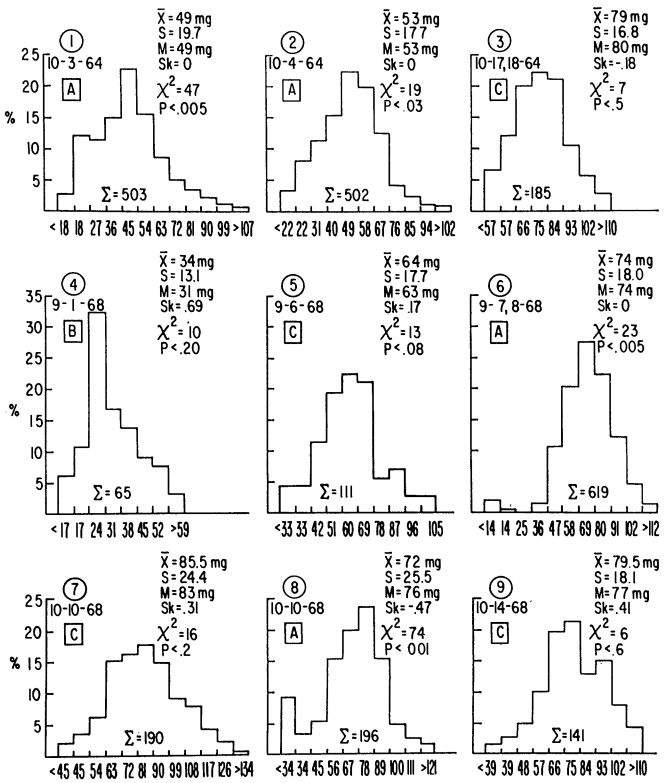



Fig. 28.—Weight frequency distribution of autumn larva collections. Ordinates: per cent larvae in each size class (all graphs to same scale). Abscissae: weight group ranges (mg). A, B and C are localities. Central figure is total number of larvae for group. S = standard deviation from mean; P = probability of normal distribution; M = median; Sk = skewness (method of Simpson and Roe, 1939, p. 143-146)

to maturity. At a larval weight of 117 mg, and having undergone at least seven molts, this animal was placed on soil and given a 16/8 hr light regimen. It emerged (in midwinter) after 20 days in its cell as an apparently normal female of *P. lucicrescens*. The time from egg hatch to eclosion was 14 months.

*Life cycle.*—Though the ontogeny from egg to adult in 14 months in the laboratory suggests the possibility of a 1-year life cycle, the actual field data argue otherwise, leaving aside the predictable cessation of growth during the months when the ground temperature is too low. The presence in routine autumn collections of larvae ranging down to 5 mm in length, along with the apparently full-grown individuals which make up the bulk of the samples, argues strongly for the presence of at least two annual broods. In the autumn also, partic-

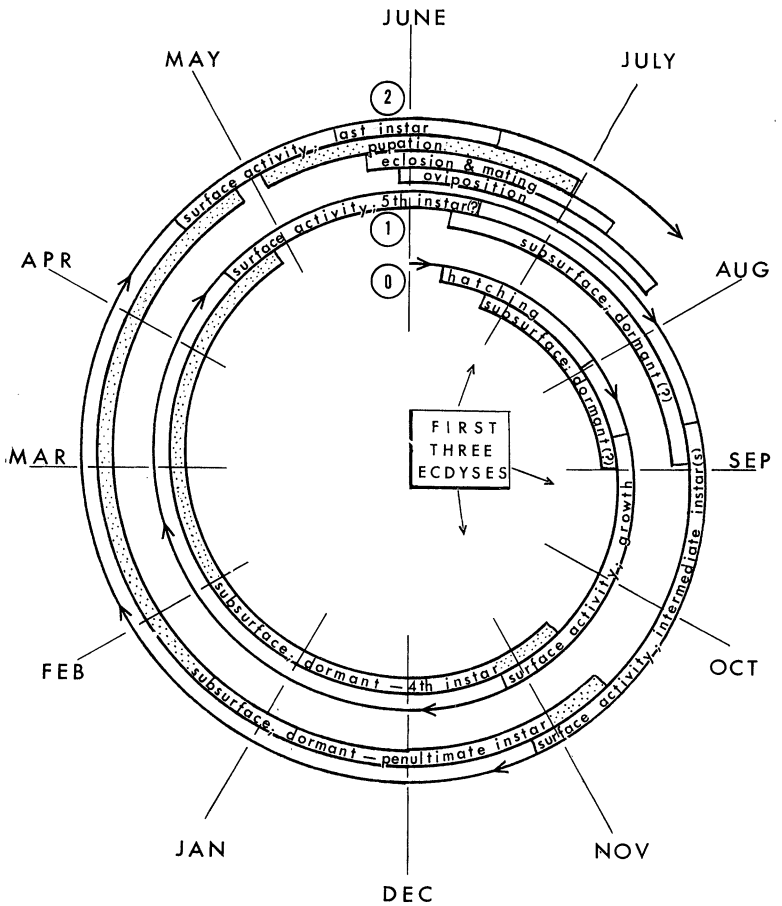



Fig. 29.—Postulated life cycle of *Photuris* in the Maryland region (clockwise starting with "0"). Circled numerals = completed years. Each labeled arc band indicates duration of given activity for the population. "Subsurface" = periods spent underground

ularly in sandy soil close to water, one occasionally comes upon a subsurface "nest" of a dozen or more tiny larvae (2-3 mm) in close proximity, apparently representing the as-yet-not-scattered hatch of one clutch of eggs. From laboratory experience an early-hatched (June) larva would be in the fourth or fifth stage by the end of summer (*i.e.*, at the age of 80-100 days) and, considering the winter dormancy, would require at least a year to reach the sixth instar. Since seven to nine molts are indicated by our limited observations and by various sources cited by McDermott (1964), completion of the life cycle within 1 year seems unlikely.

On the assumption that a population consisting of mixed yearly broods should give a size distribution with peaks corresponding to the year groups, we recorded individual body weights in nine samples of autumn larvae collected in three localities during 2 nonconsecutive years. The animals were unfed and kept at room temperature until weighing (1-25 days). Chi-square tests indicate that three of the distributions (Fig. 28) were highly significantly different from normal (Nos. 1, 6, 8). Skewness tests showed samples 1, 2 and 6 to be unskewed, 3 and 8 to have moderate negative skewness and 4, 5 and 7 to have moderate positive skewness. Part of the indicated variation may be contributed by the species mixture (*P. versicolor* and *P. lucicrescens*), habitat diversity, weather or seasonal differences, unequal skill of collecting, etc.; but it still appears that the samples were drawn from predominantly inhomogeneous populations. The three- to nearly 10-fold range in larval weights and the absence of more than one frequency peak (except possibly in Nos. 6 and 8) can reasonably be attributed to deviations in hatching time, larval nutrition, population density and the like. Since many larvae collected in early September are very large it seems likely also that there is some sort of photoperiodic cutoff of pupation-induction so that larvae that are not quite mature by early summer are deferred to the following season. We have no evidence regarding the possibility that individuals may overwinter as pupae. In sum, the evidence indicates that larvae require one full and one partial season of growth and two winter dormancies to attain maturity at the proper time in the spring (Fig. 29). Such a larval life-span of 22-24 months agrees with the deductions of Williams (1917), Hess (1920) and McDermott (1958).

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