Oecologia (Berl.) 18, 85—99 (1975)

Environmental Control of the Daily Onset of Luminescent Activity in Glowworms and Fireflies (Coleoptera: Lampyridae)

Hans Dreisig

Zoological Laboratory, University of Copenhagen, Copenhagen

Received November 12, 1974

Summary. The daily onset of activity in fireflies and glowworms is a complicated process involving both a circadian rhythm and a triggering mechanism controlled by ambient illumination. Onset of the luminescent activity has been investigated in the field and under semi-natural and experimental conditions.

1. The onset of flashing or glowing occurs at a critical low illumination during or just after the twilight period. This was determined in the adult glowworm *Lampyris noctiluca* in Denmark and in the fireflies *Photuris congener* and *Photinus umbratus* in Florida.

2. The dispersion of activity onsets differs in the three species which is partly due to differences in duration of the decrease of illumination (duration of twilight). At the long duration of twilight in Denmark, *L. noctiluca* has a greater dispersion of onsets than has *P. congener* at the short twilight in Florida, although the period of activity onsets occurs during about the same range of illuminations.

3. The onset of activity occurs at a lower illumination at low than at high temperatures.

4. At a reduction in illumination to different low values an increasing number of animals does not commence activity above about 1 lux. There is no activity if the illumination remains above 10 lux.

5. A period of latency appears in the onset of luminescent activity by a sudden change in illumination from light to dark (dim light). The duration is about 11 min in *L. noctiluca*, 5 min in three species of *Photuris* and $3^1/_2$ min in *P. umbratus*. The latency is constant at different illuminations below the threshold for overt activity. The process underlying the latency also occurs at illuminations above the threshold, but it is slowed down the higher the illumination. Further, the latency is shorter at a fast decrease of illumination than at a slow.

6. It is suggested that onset of activity in nocturnal insects involves three steps. A circadian rhythm of sensitization brings the animal into a specific state of receptivity. This happens close to the normal time of activity onset. Further, a latency process controlled by illumination occurs before overt activity can take place. This is then released below a certain threshold level of illumination.

Introduction

The change of ambient illumination occurs most rapidly during the twilight period, and many animals use this as a time-cue and start their daily phase of activity at this time. Fireflies and glowworms respond to a specific low illumination and start a period of flashing or glowing each night during the twilight period (Allard, 1931; Buck, 1937; Dreisig, 1971a; Lloyd, 1966a).

It is well established that light emission in the Lampyridae has a sexual function (Buck, 1937; Dreisig, 1971a; Hess, 1920; Lloyd, 1966a, b, 1969, 1971; McDermott, 1917; Papi, 1969; Schwalb, 1961). However, the larvae also emit light and the function of this is unknown (Dreisig, 1974). In *Lampyris* and a few

other genera the adult female is wingless and larviform. She hides during the day at the ground and appears at dusk in the low vegetation in an exposed position. Here she glows continuously until she is found by a male and copulation starts. The males fly while searching for the females, but glow only faintly or not at all. In the true fireflies both sexes have wings but normally only the males fly. The male emits a species-specific flash signal at certain intervals during the flight, while the female perches in the vegetation and only flashes in response to a flashing male.

A response to a critical low ambient illumination serves to synchronize the activity of the population, promoting the meeting of the sexes. The purpose of this study was to investigate the daily onset of activity in different species of glow-worms and fireflies in relation to illumination under natural and semi-natural conditions at different seasons and latitudes, and under experimental conditions.

Material and Methods

Species Investigated. Lampyris noctiluca Geoffr. was studied at Molslaboratoriet in Denmark. Methods and results concerning field observations on this species were reported in two previous papers (Dreisig, 1971a, 1974).

Observations on the fireflies took place at the Archbold Biological Station in central Florida. The following species were studied. *Photuris congener* LeConte is active early in the season and in 1971 it was abundant all over the area from about March 13. It disappeared in the beginning of April. *Photuris "A"* (Lloyd, 1969) is an unnamed new species that was very common from the middle of April. *Photinus umbratus* LeConte was seen first on April 29 and was active for about 3 weeks. A few observations were made on females of *Photuris versicolor*, a species in which the females also flash spontaneously.

Observations in the Field. L. noctiluca was observed in the vegetation along a road for a stretch of 200 m and time of onset and cessation of glowing was determined for each adult female in the area.

The number of flashing *P. congener* males was counted for a stretch of 30 m along a shrubbery. The weather factors were measured at the edge of the shrubbery because most of the activity took place here. The flash pattern consists of single pulses in rapid succession (about 2 flashes/sec at 20° C). The flash rate in relation to air temperature will be described in a following paper.

The number of flashing *P. umbratus* males was counted for a stretch of about 30 m between a road and a hammock. The flash pattern consists of single pulses repeated every 3.5 sec at 24° C. The flash is yellow and the flight path is close to the ground.

The illumination was measured every 2 or 5 min during the evening by a Gossen Tri-lux (10–120000 lux) and a Lange Mililuxmeter (0.001–1000 lux). The photocell was placed on the ground. Temperature, wind velocity and relative humidity were also measured. The illumination was measured as lux and converted to the logarithmic value with 10 added (log lux + 10). The use of log lux is justified both by the enormous daily variation in light intensities and by Weber-Fechner's law concerning the sensitivity of the eye. The use of logarithms does not produce a linear relation with time, but for small intervals (minutes) the decrease in illumination can be regarded as linear. Means and standard deviations can be calculated if the distribution of the log values is normal. When log values are subtracted it has been given a special designation, dlx.

Experimental Procedure. The animals were kept singly in glass jars with some vegetation, the glowworms in 1 l jars and the fireflies in 10 l jars. The jars were placed in a darkroom illuminated during the daytime by three 150 watt incandescent lights at a distance of about 1.5 m. This provided an illumination of 180 lux at the place of the jars. A dim illumination of 0.1 lux was used during the dark period because total darkness usually inhibits the activity. The illumination was changed by reducing the voltage to the lamps. At a gradual decrease, the illumination was reduced at a constant rate according to a logarithmic scale and the

rate of change expressed as the differece in log lux per unit time, dlx/min. The temperature was kept at 22° C in Denmark and at 26° in Florida. All experiments were done at the normal time of activity in the evening.

The animals were also placed under semi-natural conditions, exposed to a natural variation of illumination and temperature. In this way they were exposed directly to the illumination from the sky and the releasing light value could be determined more accurately than in the field were the animals experience different light conditions at their hiding places.

Results

The Critical Illumination

Lampyris noctiluca. The critical illumination is defined as the illumination at the time when 50% of the population has commenced activity (Dreisig, 1971a). This is the median of the frequency distribution of activity onsets. The frequency distribution of onsets is converted to cumulative percentages which in the investigated species shows sigmoid curves indicating normality (Fig. 2). This means that mean and median are practically identical. The critical illumination in the field in *L. noctiluca* was 1.3 lux (10.11 log lux + 10) (Table 1 and Fig. 2).

The result under semi-natural conditions was the same as in the field in cases where the jars were provided with vegetation in which the animals could hide when not glowing. The median critical illumination in 87 observations was 1.5 lux (10.17 log lux + 10). If the jars were not provided with vegetation and the animals directly exposed to the illumination, the critical illumination was considerably lower, 0.28 lux (9.45 log lux + 10) (Table 1). This difference might be due to the illumination being lower beneath the vegetation than at the place of glowing where the light was measured in the field. If the releasing illumination is reached while the animal is hiding, it experiences an increase in illumination when it climbs into the vegetation. The observed critical illumination is therefore higher than the actual releasing illumination below the vegetation. The fireflies rest in more exposed positions and their latency period is short, hence a better agreement between observations in the field and under semi-natural conditions (see below).

Table 1. The onset of luminescent activity in three species of Lampyridae in the field and under semi-natural conditions. The critical illumination occurs at the median of the cumulative frequency distribution of onsets. The dispersion of onsets is expressed by the standard deviation (s) is relation to time (min) and illumination (dlx)

	Critical illumination		Dispersion of onsets		N	Twilight min	Mean temp. °C
	min after sunset	log lux+10	min	dlx			
L. noctiluca							
Field	63	10.11	13.7	0.48	271	64	11.5
Semi-natural	81	9.45	15.1	0.49	12	64	12
P. congener							
Field	19	9.40	3.4	0.37		24	19
Semi-natural	34	9.38	5.8	0.53	10	23	20
P. umbratus							
Field	18	10.00	1.2	0.14		25	24.5
Semi-natural	16	10.59	3.4	0.33	10	26	24

The larvae of *L. noctiluca* commenced activity at a considerably lower illumination than the adults. The critical illumination was 6.85 log lux + 10 (Dreisig, 1974).

Photuris congener. The onset of luminescent activity in the fireflies cannot be determined in the field in the same way as in *L. noctiluca*. It is not possible to determine the time when the whole population has started to flash because the animals are not stationary. However, it was decided to estimate the time of maximum activity following the initial increase as the time of 100% onset of activity. In *L. noctiluca* the average range of onsets was 49 min, while the maximum number of animals was observed 40 min after the first was seen. The difference is due to animals that cease to glow before the whole population has started. Since the range of onsets in the fireflies is small, as seen under semi-natural conditions, a possible error cannot be more than a few minutes. Further, since the curves of cumulated percentages are sigmoid, the effect on the median will be small. Values between 0 and 100% are calculated by cumulating the percentage increase in activity per minute (Fig. 1).

The critical illumination was 0.25 lux (9.40 log lux + 10) (Table 1 and Fig. 2). As will be shown later, the critical illumination depends on the temperature. Accordingly, Table 1 and Fig. 2 only include observations at temperatures of $20 \pm 2°$ C. The critical illumination under semi-natural conditions was 0.24 lux (9.38 log lux + 10) in agreement with the field observations.

Photuris "A" was observed for three days in the field. The critical illumination was about the same as in *P. congener*, 0.38 lux (9.58 log lux + 10).

Photinus umbratus. Although this species was only observed on one evening in the field, it seems that it starts to flash at a higher illumination than the *Photuris* species. The critical illumination was 1.0 lux (10 log lux + 10) (Table 1 and Fig. 2). It also started to flash at a high illumination under semi-natural conditions, the average was 4.0 lux (10.59 log lux + 10). It was interesting that the duration of activity in this species was much shorter than in the *Photuris* species, all activity ceased after about 20 min, while in the others it lasted several hours.

The Dispersion of Activity Onsets

In studies of crepuscular activities it is often necessary to compare activities at different seasons and places. This, however, is difficult, because time of sunset and duration of twilight varies during the year and with the latitude. If the timing of activity onsets is controlled by the illumination, a comparison is not possible if it is described by means of conventional time-units. The activity must either be related to the crep-unit (Nielsen, 1963) or directly to the illumination.

In Fig. 1 is shown the onset of activity in *P. congener* in March in Florida and in *L. noctiluca* in June in Denmark. The time-scale shows minutes after sunset. It is seen that the times of activity onset are very different in the two species. In *P. congener* the critical illumination occurred 19 min after sunset while in *L. noctiluca* it occurred 63 min after sunset.

The dispersion of activity onsets also differed considerably in the two species in relation to time (Fig. 1). The standard deviation has been chosen in these

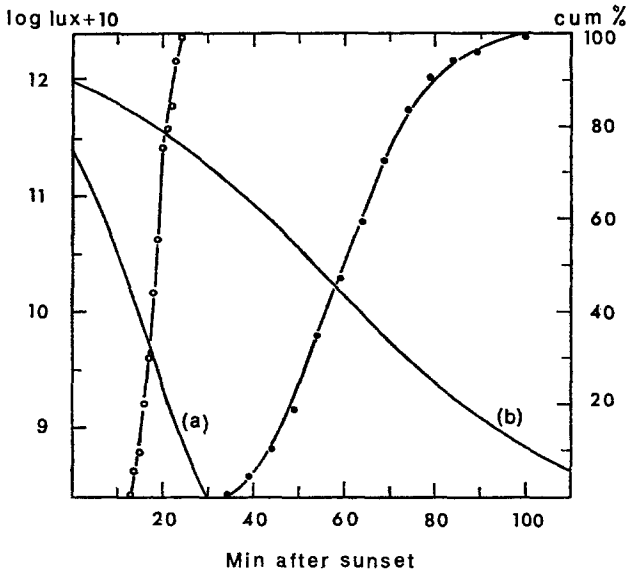

Fig. 1. Onset of luminescent activity in the field in *Photuris congener* males (o—o) in Florida (5 days in March 1971) and in *Lampyris noctiluca* females (•—•) in Denmark (12 days in June 1969). The average illumination in Florida (*a*) and in Denmark (*b*) during the observation periods is shown. Sunset in Florida was at 18h40 and twilight lasted 23–24 min, while in Denmark sunset was at 21h10 and twilight lasted 64–65 min

studies as a measure of the dispersion. The dispersion was 3.4 min in *P. congener* and 14 min in *L. noctiluca*. In *P. umbratus* it was only 1.2 min. The observations under semi-natural conditions agree well with this (Table 1).

In Fig. 1 is also shown the average illumination, and it is seen that the decrease of illumination occurs much more rapidly in Florida than in Denmark. The duration of the twilight period is a good expression of the rate of change of illumination. This was 23–24 min in Florida and 64–65 min in Denmark during the observation periods (twilight is the period during which the center of the sun moves from 0° 50′ to 6°00′ below the horizon).

The difference in rate of change of illumination due to season and latitude affects the time and dispersion of activity onsets. It will be seen that the critical illumination occurs at a later time in relation to sunset, the slower the decrease of illumination. Further, it seems correct to assume that if the period of activity onsets in a population occurs during a certain range of illuminations, the duration of this period is shorter at a short twilight than at a long one. In other words, there should be a negative correlation between dispersion of onsets and rate of change of illumination.

This might explain some of the difference concerning dispersion of onsets between *L. noctiluca* and *P. congener*. Fig. 2 shows the onset of activity in three different species in relation to illumination irrespective of the time. It is seen that the difference between the dispersions in *L. noctiluca* and *P. congener* is much smaller when the onsets are related to the illumination than when they are related

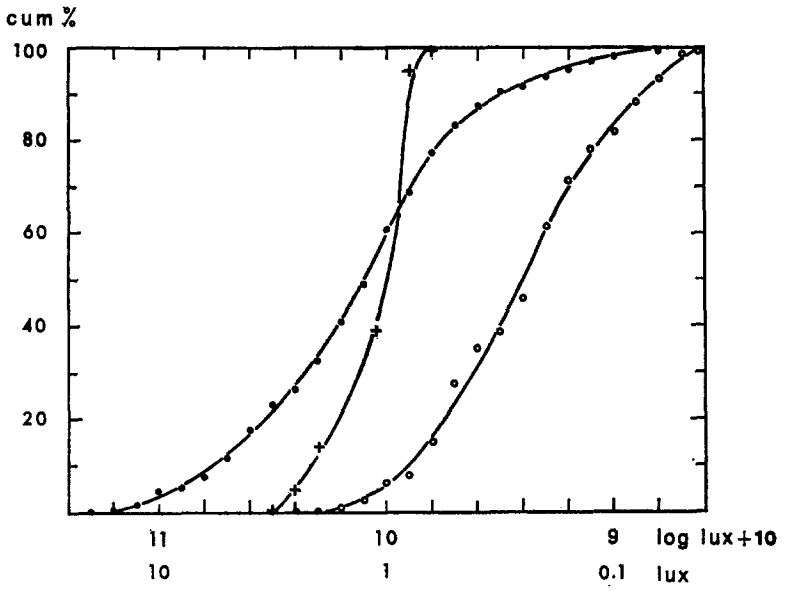

Fig. 2. Onset of luminescent activity in the field in *Lampyris noctiluca* females (•—•), *Photuris congener* males (o—o) and *Photinus umbratus* males (+—+) in relation to ambient illumination during and after the evening twilight. See also legend to Fig. 1. *P. umbratus* was observed on April 29, 1971, in Florida

Table 2. The critical illumination and dispersion of activity onsets in *Photuris congener* at different experimental decreases of illumination

Rate of decrease dlx/min	Critical illumination log lux +10	Dispersion (s) min	N
0.05	10.25	4.5	11
0.10	10.30	4.5	23
0.15	10.40	3.1	10

to the time. The onsets occur during about the same range of illuminations in both species. However, the glowworm still has a greater dispersion than the firefly. The dispersion in relation to illumination under semi-natural conditions was practically the same in both species (Table 1).

The onset of activity in *P. umbratus* occurred very rapidly during a narrow range of illuminations (Fig. 2). The disperison in relation to illumination was much smaller than in the two other species.

The illumination was decreased gradually under experimental conditions at three different rates according to a logarithmic scale. *P. congener* started to flash at about the same critical illumination at all three rates (Table 2). The small differences are not significant. The dispersion was the same at rates of 0.05 and 0.10 dlx/min ($s = 4.5$ min), but at 0.15 dlx/min it was significantly smaller (3.1 min). At a sudden change from light to dark it was only 1.93 min. Under field conditions the dispersion was 3.5 min. However, the rate of decrease is not

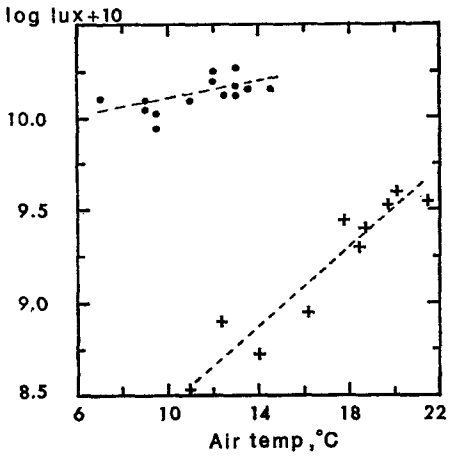

Fig. 3. Scatter plot showing relation between air temperature and critical illumination at the daily onset of luminescent activity in field populations of *Lampyris noctiluca* (•) and *Photuris congener* (+). Stipled lines show linear regressions

constant in the field (maximum rate is 0.12 dlx/min at a twilight period of 24 min), and a comparison is not possible. Experiments with *P. umbratus* showed that also in this species did the dispersion of onsets become smaller, the faster the rate of change of illumination. The dispersion was always smaller than in *P. congener* at the corresponding rate.

Effect of Temperature on the Critical Illumination

Buck (1937) mentions that *Photinus pyralis* starts to flash earlier at higher than at lower temperatures. This is also seen in *P. congener* and in *L. noctiluca* (Fig. 3). The correlation of illumination at onset of activity to temperature is highly significant in the firefly ($r = 0.95$), while in the glowworm it is significant at the 0.05 level ($r = 0.57$).

The Period of Latency

Sudden Change of Illumination. In a number of nocturnal insects it has been shown that the activity does not start until a certain period of time has passed since the change from light to dark (Nielsen and Nielsen, 1962; Nielsen and Dreisig, 1970). The experiments reported below were intended to determine this latency in the luminescent activity of glowworms and fireflies, and to investigate its dependence on external factors.

The period of latency was determined in five different species at a sudden transition from light to dark (0.1 lux) at the normal time of activity (Table 3). The mean latency in *L. noctiluca* was 11.1 min (curve c in Fig. 4). During the latency period the female appears and takes up a characteristic position in the vegetation. In the fireflies the period of latency was shorter than in the glowworm. In three species of the genus *Photuris* it was about 5 min. Curve b in Fig. 4 shows the onset in *P. congener*. In *P. umbratus* the average latency was

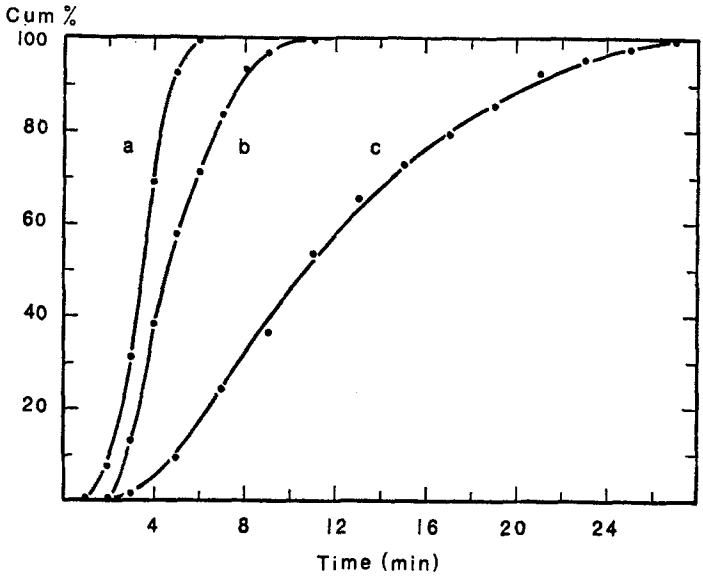

Fig. 4. Onset of luminescent activity in *Photinus umbratus* (*a*), *Photuris congener* (*b*) and *Lampyris noctiluca* (*c*) following an abrupt change of illumination from 180 lux to dim light of 0.1 lux. No of obs.: see Table 3

Table 3. Duration of the latency from a sudden light-dark change (180 to 0.1 lux) to onset of glowing or flashing in different species of Lampyridae

	Mean min	Dispersion (*s*) min	*N*
Lampyris noctiluca	11.1	5.4	136
Photuris congener	4.9	1.9	31
Photuris "A"	5.0	2.3	18
Photuris versicolor	5.3	2.0	6
Photinus umbratus	3.4	1.1	13

only 3.5 min (curve a in Fig. 4). The differences between these three means are highly significant. The dispersion of onsets was greatest in *L. noctiluca* and smallest in *P. umbratus* while the *Photuris* species were intermediate (Table 3).

L. noctiluca was also subjected to changes from "full light" to different low illuminations. From Table 4 it is seen that the latency is about the same over a range of illuminations from 0.001 to 2.5 lux. The animals did normally not start to glow in total darkness (older individuals were, however, able to do this). At 2.5 lux the onset was slightly delayed; however, the mean at 2.5 lux is not significantly different from the means at the lower illuminations. If the illumination was reduced to 10 lux or to any illumination above this, no one appeared and started to glow. The number of animals that started to glow decreased the higher the illumination. At 0.1 lux all started to glow, but at 2.5 lux about half of the animals did not start at all and at 10 lux no one did so. This clearly indicates that a threshold is involved. If the illumination is below the threshold

Table 4. Duration of the latency after a sudden change from light (180 lux) to different low illuminations (column 1) to onset of glowing in *Lampyris noctiluca*

Illumination		Mean latency min	Dispersion (*s*) min	No. started
lux	log lux +10			
10	11.0	—		0/6
2.5	10.4	18.5	8.8	8/14
1.0	10.0	11.3	5.3	14/15
0.1	9.0	11.1	5.4	136/136
0.008	7.7	13.5	5.0	10/12
0.001	7.0	18.2		5/6
0		—		0/10

the latency is about the same, but if it is above, the animal will not commence activity, although some appeared and climbed into the vegetation without luminescing. The experiments reported above demonstrate the individual variation of this threshold and that the number of animals that does not commence activity increases at illuminations from about 0.1 to 10 lux. At 2.5 lux about half does not start, so this must be about the average threshold illumination corresponding to the critical illumination observed in the field and under semi-natural conditions.

P. congener was subjected in the same way to a change of illumination to 10, 8, 6.3, 4 or 0.1 lux. Although the number of observations was small, it was evident that also in this species did the number of animals that commenced activity decrease the higher the illumination. At 0.1 lux all animals started to flash, while at 4 lux only 50% were able to do so. At 6.3 and 8 lux only 1 out of 6 animals started to flash regularly, and at 10 lux no one started.

Light Change with Gradual Transition. It is clear that if the illumination decreases gradually, as under natural conditions, the latency period must occur at illuminations above the one at which overt activity starts. *L. noctiluca* was subjected to different low illuminations above the threshold for overt activity: 6.3, 10, 15, 20 or 25 lux, and these were kept on for 15 min. The latency period will then be wholly or partly completed if it is initiated by any of these illuminations. Upon subsequent transfer to dim light below the threshold (0.1 lux) the animals will then start to glow immediately or after a time that is shorter than a normal latency. Fig. 5 shows the average onset in dim light, and it is seen that the lower the preceding illumination had been, the shorter is the latency in dim light. An analysis of variance shows that the means differ significantly from each other ($P < 0.001$).

P. congener was exposed to different low illuminations for only 5 min. The light was then reduced to 0.1 lux. As seen from Fig. 6 the result is comparable to that obtained with the glowworm, and also in this case do the means differ from each other ($P < 0.001$). *P. umbratus* behaved in the same way, except that the latencies in dim light were shorter than in *P. congener* (Fig. 7). An analysis of variance shows that the means differ significantly ($0.001 < P < 0.01$).

In some experiments the illumination was decreased at different rates and halted at a certain level for 5 min. The light was then reduced abruptly to 0.1 lux, and the onset of activity was observed. *Photuris* "*A*" was exposed

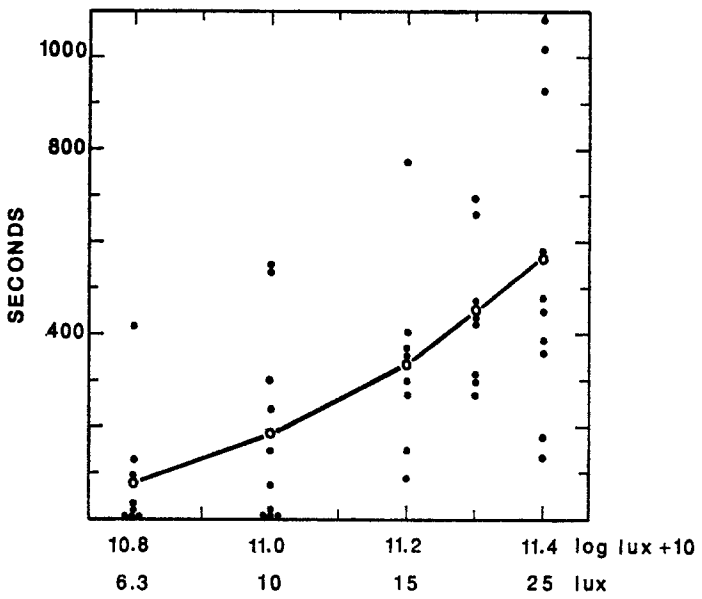

Fig. 5. Onset of glowing in *Lampyris noctiluca* in dark (dim light of 0.1 lux). The light was changed from 180 lux to different low illuminations (abscissa), and these were kept on for 15 min before the light was reduced to 0.1 lux. The points represent individual onsets after the transfer to 0.1 lux (ordinate). The lines connect the average onset for each illumination

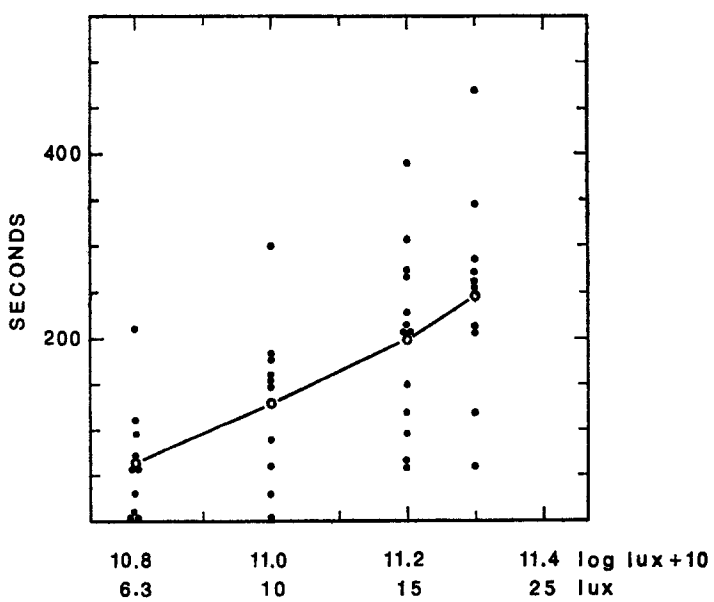

Fig. 6. Onset of flashing in *Photuris congener* in dark (dim light of 0.1 lux). Experimental procedure as explained in the legend to Fig. 5 except that the different low illuminations (abscissa) were only kept on for 5 min

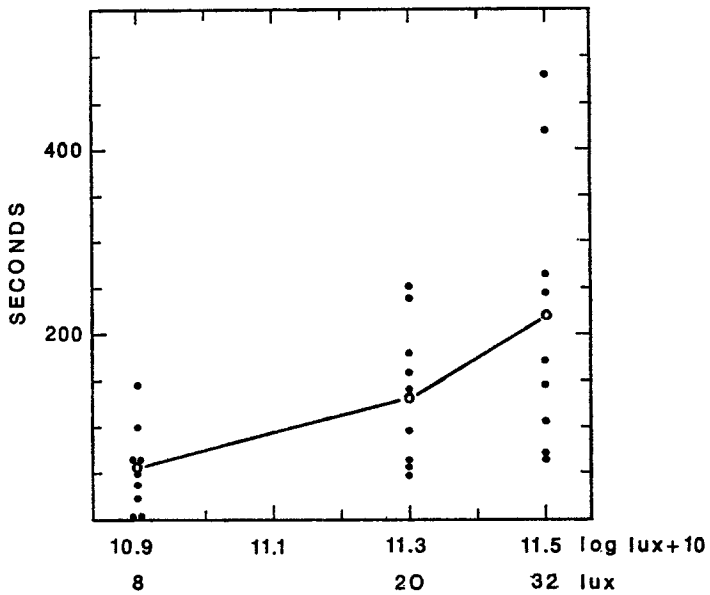

Fig. 7. Onset of flashing in *Photinus umbratus* in dark (dim light of 0.1) lux. Experimental procedure as explained in the legend to Fig. 5 except that the different low illuminations (abscissa) were only kept on for 5 min

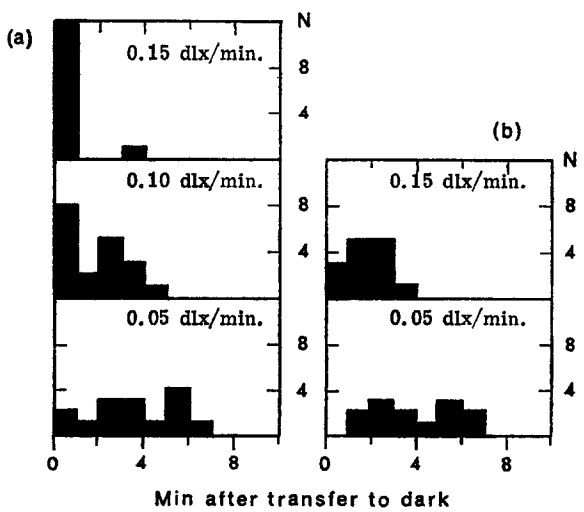

Fig. 8a and b. Onset of flashing in *Photuris congener* (a) and *Photinus umbratus* (b) in dark (dim light of 0.1 lux) following a gradual decrease of illumination from about 200 lux to 12 lux. The illumination was kept at 12 lux for 5 min before being reduced abruptly to 0.1 lux. The decrease of illumination occurred at a fast rate (0.15 dlx/min), at an intermediate rate (0.10 dlx/min) or at a slow rate (0.05 dlx/min)

Table 5. Duration of the latency from a light-dark change to onset of glowing in *Lampyris noctiluca* at different temperature conditions. The temperature was changed 20–30 min before the light change

Temperature (°C)	Mean latency (min)	Dispersion (s) (min)	N
13° constant	—		8
22° constant	11.1	5.4	136
31° constant	10.9	5.5	10
31° to 22°	10.3	4.6	20
31° to 13°	14.4	6.6	14
22° to 13°	17.6	8.1	16
22° to 31°	24.0	11.9	10
19° to 31°	31.4	15.7	10
13° to 22°	31.1	15.2	14
13° to 27°	42.1		7
13° to 31°	—		10

to three different rates and the decrease was halted at 12 lux for 5 min (Fig. 8a). Following a fast decrease (0.15 dlx/min) almost all animals started to flash just after the transfer to dim light, but following a slow decrease (0.05 dlx/min) most of them started to flash considerably later. The result was intermediate following a rate of 0.10 dlx/min. *P. umbratus* was exposed to two different rates (Fig. 8b). Following a fast decrease of illumination the average onset in dim light occurred considerably earlier than after a slow decrease. This difference is highly significant.

Effect of Temperature on the Latency. The period of latency in *L. noctiluca* was investigated at different temperature conditions (Table 5). At constant 22° or 31° the latency was about the same. At constant 13° no one started to glow, although in the field glowing was observed at 6.5°, and also in the laboratory did the animals glow at 13° if they were transferred from a higher temperature than 13°. This indicates that the ability to glow at 13°, or at lower temperatures, is an effect of high temperatures during the preceding period. In some experiments the temperature was changed 20–30 min before the light change. At a temperature step-down the latency was about the same as at constant temperatures. At an increase of temperature the latency became longer, and this was more pronounced the greater the step-up. At the same time more animals did not glow, and if the temperature was increased from 13° to 31° no one started to glow.

Discussion

A persistent daily rhythm is often regarded as being the result of an endogenous physiological rhythm with a period of about 24 hrs that is being reset daily by an external signal, most likely a light change at dusk or dawn (Aschoff, 1960). The mechanism of entrainment by external factors is an important one in this context. Under natural conditions the change of illumination around sunset and sunrise is one of the most constant and conspicuous features of the environment. The time and duration of this transition change only slowly

with the season and latitude. Many animals use this as a time-cue and start a period of activity at sunset or sunrise at specific low illuminations (Dreisig, 1971a; Nielsen and Nielsen, 1963; Persson, 1971). These illuminations occur during the twilight period when the rate of change of illumination is greatest. It is interesting to note that both the glowworms in Denmark and the fireflies in Florida start the luminescent activity at this time at a critical illumination of about 1 lux (Fig. 2). This is also the case in a number of species of Noctuids (in progress).

It was found that the dispersion of the activity onsets is partly controlled by the rate of change of illumination. The slower the rate of change, the greater is the dispersion. This is a consequence of the range of onsets being restricted to a certain range of illumination (see p. 89).

The light emission of Lampyrids can be compared with other endogenously controlled activity rhythms that are free-running under constant conditions, but normally are entrained to a light-dark cycle (Dreisig, in prep.). Aschoff and co-workers have shown that the phase relationship between activity and "Zeitgeber" depends on a number of factors, the most important being the LD ratio, the level of illumination during the light and dark periods, the duration of twilight and the spontaneous frequency (Aschoff, 1969; Wever, 1967). Investigations on insects concerning this are few (Lamprecht and Weber, 1971; Lohmann, 1964). In mammals and birds the phase difference changes in a predictable way during the year, which means that the onset of activity in these animals is not bound to a specific illumination. The present study indicates that a different mechanism is at work in nocturnal insects commencing the activity during the twilight period and in which the activity normally is completely prevented in light above a threshold level. The release of activity depends on a process controlled by specific conditions of illumination and the phase relationship is stable within wide variations of the environmental cycle (Dreisig, in prep.). Most insects are short-lived and can not be studied during a whole year, but observations on the flying activity of *Plusia gamma* (Noctuidae) during a summer also support this assumption. Of course, these animals might adapt to different critical illuminations as has been observed in Noctuids under arctic conditions with midnight sun (in progress). Abnormal phase positions are also observed at extreme light cycles when the signal occurs during the refractory period. Also hunger and low temperatures at night can displace the activity in nocturnal insects (Dreisig, 1971b, Nielsen and Dreisig, 1970). Normally, the activity is released by specific light conditions, and a physiological model is proposed comprising the following three steps.

(1) The release of activity depends on an endogenous circadian rhythm of sensitization. The animal has to be in a certain state of receptivity if an external signal is to be effective. This is only reached close to the normal time for onset of activity. This aspect of the mechanism will be further discussed in a following paper (Dreisig, in prep.).

(2) At a change from light to dark a period of latency occurs which must be terminated before activity can start. In nature, during the gradual change of illumination at twilight, this element is not apparent. It has to be studied by

experiments where there is a sudden change of illumination and then appears as a delay of the activity onset. This is discussed below.

(3) If the animal is sensitized and the latency process completed, overt activity takes place when a certain threshold illumination is reached, the critical illumination.

An unknown physiological process is thought to take place during the period of latency. This might consist in a release of inhibition of the controlling nervous center and pathway, or it might have something to do with the process of dark adaptation. The latter is now being investigated. It is controlled by external factors, especially the level and rate of change of ambient illumination. The process is normally prevented by bright light but is initiated by low illuminations. It has been shown that if the illumination is changed to different low levels, the rate of the process is faster, the lower the illumination (Figs. 5–7). Below about 1 lux it occurs at a maximum rate and is terminated in about 11 min in the glowworm and 5 min in the fireflies (*Photuris*) (Fig. 4). It will be seen that the level below which the process is terminated in the shortest possible time corresponds to the threshold below which overt activity is possible. During a gradual decrease of illumination at twilight, the rate of the process increases with decreasing light intensity, and it is probably concluded at the same time or shortly before the threshold illumination is reached.

Some preliminary experiments indicate that the process is faster at a rapid decrease of illumination than at a slow (Fig. 8). The effect of this might be to synchronize the time of termination of the latency period with the critical illumination. If the level of the illumination was the only factor controlling the duration of the latency, the animals would not be able to adjust to different durations of twilight. The onset would be delayed in relation to the threshold in case the decrease of illumination occurred too rapidly, while the latency would be terminated too early if the decrease occured too slowly.

Acknowledgments. The author wishes to acknowledge the support of persons and institutions concerned with this study. Grants from the Danish State Research Foundation and from the University of Copenhagen permitted me to travel to Florida. I extend my sincere thanks to Mr. Richard Archbold for his help and generous hospitality, and to the staff of the Archbold Biological Station. In particular, I should like to thank Mr. C. E. Winegarner for help in collecting animals in the field. Dr. James Lloyd, University of Florida, Gainesville, very kindly identified the investigated firefly species. I am grateful to Dr. E. Tetens Nielsen for much help and for critically reading the manuscript, and to Professor H. M. Thamdrup for placing the facilities of Molslaboratoriet at my disposal.

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Dr. Hans Dreisig
Zoological Laboratory
University of Copenhagen
Universitetsparken 15
Copenhagen Ø, Denmark