

DET KGL. DANSKE VIDENSKABERNES SELSKAB

BIOLOGISKE MEDDELELSER, BIND XXI, NR. 4

---

ACTIVITY AND MIGRATION OF  
*PLUSIA GAMMA* L.

STUDIES ON THE ACTIVITY OF INSECTS III

BY

ELLINOR BRO LARSEN



KØBENHAVN

I KOMMISSION HOS EJNAR MUNKSGAARD

1949

DET KÖN. DANSKE VIDENSKABERNE SÆLSKAB  
BIOLOGISKE MEDDELELSER, NR. XXI, 1911

---

ACTIVITY AND MIGRATION OF  
PLESIA GAMMA L.  
STUDIES ON THE ACTIVITY OF INSECTS III

BY

ELLENOR BRO LARSEN



KØBENHAVN

KOMMISSIONERNE HOS HANS HENSCH

Printed in Denmark

Bianco Lunos Bogtrykkeri

## I. Introduction.

*Plusia gamma* and a few other species occupy a place apart among the noctuids in that they are active both by day and by night (cp. HERING, 1926 p. 131 and others). *P. gamma* has attracted attention also by its occurrence in large numbers in certain localities, and it is one of the oldest migrating *Lepidoptera* known.

A large number of observations have been published concerning *P. gamma*'s migratory habits (WILLIAMS 1930, FRAENKEL 1932, FISHER 1938, WILLIAMS, COCKBILL, GIBBS, DOWNES 1942, PALMÉN 1947 et alii), but studies of its behaviour under controlled conditions and field observations in relation to influencing factors have been scarce.

The present investigation is an attempt to throw light on certain aspects of the latter problems. Aware of the fact that her arguments ought to have been better supported by experiment the author has nevertheless decided to publish her paper now as in Denmark an occurrence of *P. gamma* in large numbers as that in 1946 can only be expected at long intervals.

In 1938 and subsequent years the activity of noctuids was investigated at the laboratories of Pilehuset (North Zealand), Skallingen (Southwest Jutland) and Tipperne (West Jutland) (LARSEN 1943, LARSEN 1950). The investigations included observations of *P. gamma*, which were continued at the Mols laboratory (East Jutland) in 1943 and 1946, and completed in August 1946 at Pilehuset.

## II. Experiments on Temperature Preference.

In September, 1939, at Pilehuset, the typical autumn species: *Orthosia circellaris* Hufn, *Agrotis xantographa* Fabr., and *Agrotis c-nigrum* Linn., *Xanthia fulvago* Linn., *Xanthia lutea* Strøm, and *Calocala nupta* Linn. were observed to be coming to sugar bait every night, *P. gamma* was observed with them on only one or two, particularly warm nights. The lowest temperature at which *P. gamma* was observed on bait was 16° C (Sept. 6th, cp. LARSEN 1950); as it was lively by day in the sun and also known to be active at night, the reason why it seldom accompanied the species mentioned above presumably was that it preferred a different temperature.<sup>1</sup>

In August 1943 at Mols *P. gamma* was occasionally observed together with *Amphipyra tragopoginis* Linn. during the night, but it was chiefly active by day in the sun. During these two periods experiments on the temperature preference of *P. gamma* were made which also served as a basis of comparison with the species associated with which it flew by night. In both cases individuals of *P. gamma* were collected in the day-time on heather, the other noctuids on sugar bait, and during each experiment one individual from each of the two species compared were in the apparatus at the same time. In 1939 the air humidity in the apparatus was as near as possible 100 per cent, in 1943 75 per cent.<sup>2</sup>

Fig. 1a and b show the results of the experiments. It appears that in August 1943 (fig. 1b) the temperature preference of *P. gamma* was 30° C, while *Amphipyra tragopoginis* preferred a temperature of about 16° C, which is about the average night temperature of the season.

In September 1939 (fig. 1a) the preference of *P. gamma* was found to be 25° C, while the other species (the average of the three species: *A. c-nigrum*, *A. xantographa* and *O. circellaris*)

<sup>1</sup> In general, *P. gamma* is seldom found on sugar bait except when there is a shortage of food on account of the large numbers, as was the case in Denmark in 1946, when it was observed by a number of lepidopterists.

<sup>2</sup> The experiments were made with a temperature gradient apparatus (HERTER 1924, p. 27). Like many experiments of this kind they must be viewed with some reservation as the environment offered by a "temperatur-orgel" is very different from that natural to the animals and hence may influence the result to some extent.

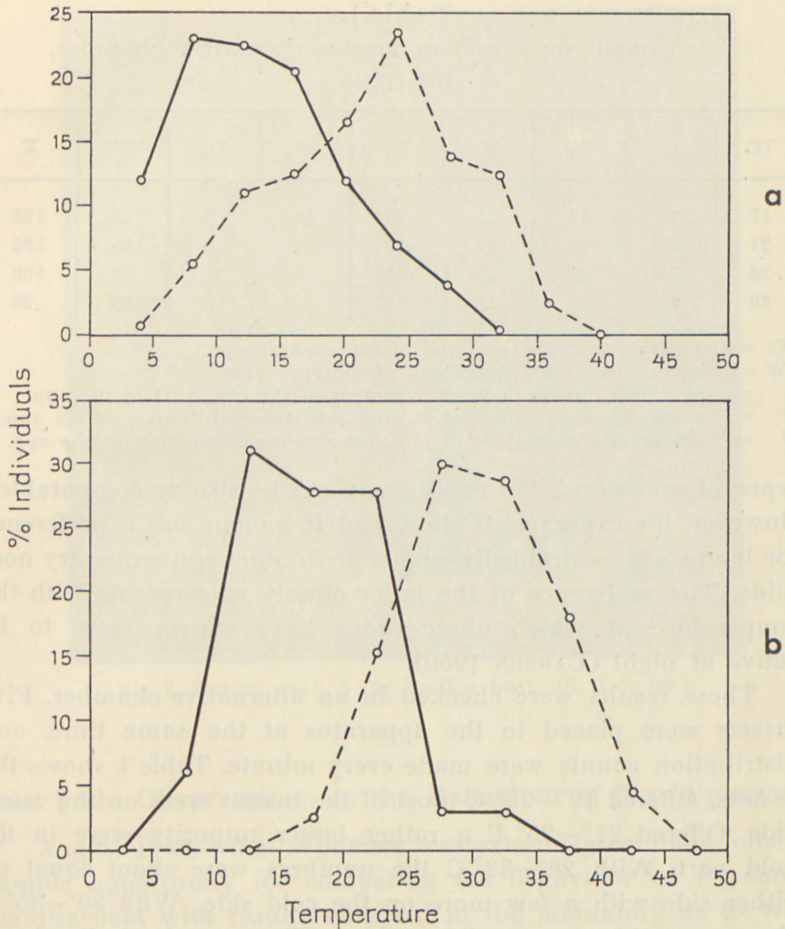


Fig. 1. (a) Temperature preference experiments in 'temperatur-orgel' on *Plusia gamma* and the late autumn species, September 1939. — *Plusia gamma*, --- *Orthosia circellaris* + *Agrotis xanthografa* + *Agrotis c-nigrum*. — (b) Temperature preference experiments with *Amphipyra tragopoginis* and *Plusia gamma*, August 1943. — *Plusia gamma*, --- *Amphipyra tragopoginis*.

showed a preference for about 12° C, which is the prevailing night temperature of the season when conditions are favourable. *P. gamma*'s preferred temperature being lower in September and extended further towards the cold side may be due to the fact that we were dealing with the last stragglers of the population, and further, a temperature adaptation may have taken place (in any case, as the experiments were carried out with two different

Table I.  
Experiments on *Plusia gamma* in alternative chamber,  
July 1946.

TC	C	%	M	%	W	%	TW	Σ
17	17	14	25	20	83	66	25	125
21	31	23	24	18	80	59	25	135
26	75	47	25	16	60	38	32	160
30	15	58	11	42	0	0	35	26

TC = temperature at the cold end of the apparatus.

TW = temperature at the warm end of the apparatus.

C = number of observations of *P. gamma* in the cold part of the app.

M = number of observations of *P. gamma* in the middle part of the app.

W = number of observations of *P. gamma* in the warm part of the app.

types of apparatus, the results may not be strictly comparable). However, the experiments show that *P. gamma* has a preference for temperatures decidedly higher than other contemporary noctuids. The preference of the latter closely corresponds with the temperature at which observations have shown them to be active at night (LARSEN 1950).

These results were checked in an alternative chamber. Five insects were placed in the apparatus at the same time, and distribution counts were made every minute. Table 1 shows the results. Offered 17°–25° C most of the insects were on the warm side. Offered 21°–25° C a rather larger minority were in the cold part. With 26°–32° C the numbers were about equal on either side with a few more on the cold side. With 30°–35° C the warm side was totally avoided. These results indicating a preferendum between 25° and 30° C are consistent with those obtained with the gradient apparatus.

Apart from the species being dependent on temperature and needing more heat than contemporary species, it is not evident what the high figures for temperature preference mean, as the insects soon die when constantly exposed to such high temperatures. The insects presumably react as if they were exposed to the radiant heat of the sun, while in the laboratory they are influenced by the high air temperatures. Further the high degree of vertical fluctuations in temperature in nature is of a certain importance.



Fig. 2. Station no. 5, a big heather bush. (E. B. L. fot.)

### III. Field Observations on the Behaviour of *Plusia gamma*.

August 1946, when *P. gamma* was extremely common, offered ample opportunity for comparing the behaviour of *P. gamma* in the field with results obtained in the laboratory as to temperature preference and activity pattern.

Observations were made at the Pilehuset laboratory. Nine stations were chosen where counts were taken every two hours except at 1 a. m.—5 a. m. (cp. PARK 1935, p. 169, and LARSEN 1943, p. 353). The first station was 3 m<sup>2</sup> of a field of flowering clover, the second a cluster of flowering *Chamaenerium angustifolium*, and stations 3—9 groups of flowering heath, *Calluna vulgaris* (Fig. 2 shows station no. 5). Temperatures were measured by means of distance thermo-couples at the top of the heath, under foliage, and at places with free radiation at heights of 2, 8 and 15 metres. An ordinary thermograph registering the varying temperatures during the period of observation was placed at station no. 5.

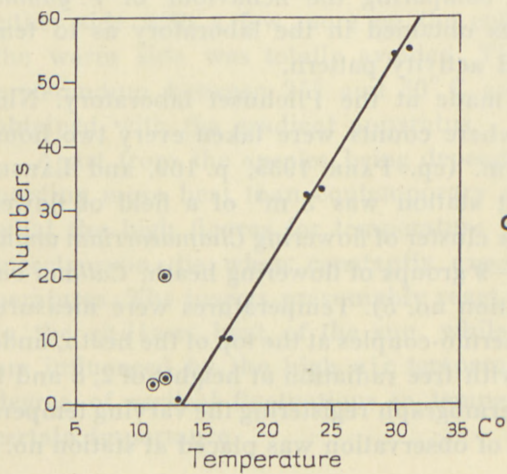
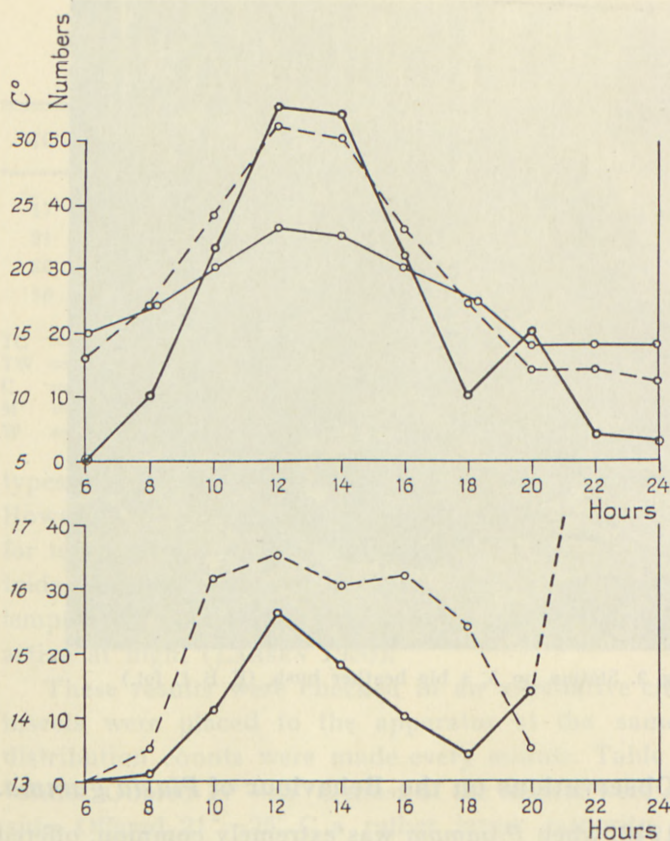


Fig. 3. (a) The average feeding activity of *Plusia gamma* at stations I-IX during 8 days and nights.

— Number of *Plusia gamma*, --- Temperature among the heather flowers, — Temperature at a height of two metres.

(b) The average activity for 10 days and nights of feeding *Hydroesia nictitans* Bhk. on *Tanacetum vulgare*. — Number of *Hydroesia nictitans*, --- Temperature measured in the weather box, Tipperne 1941. — (c) Relation between *P. gamma*'s activity and temperature.

• Daytime observations, ○ Observations at dusk.



Table II.

Counts of *Plusia gamma* from  $^{10}/_8$ — $^{16}/_8$ , the temperature being measured at the top of the heather.

Time .....	6	8	10	12	14	16	18	20	22	24	2
Date											
Numbers .....	..	..	..	..	36	28	9	<b>14</b>	11	9	..
Temp. ....	..	..	..	..	34	21	17	<b>14</b>	17	16	0
Numbers .....	..	..	28	96	101	75	10	<b>11</b>	1	1	0
Temp. ....	..	..	24	43	37	24	16	10	8	7	..
Numbers .....	0	35	51	67	..	21	13	<b>23</b>	7	5	8
Temp. ....	8	18	28	32	..	21	19	15	15	14	14
Numbers .....	1	9	49	51	38	21	2	<b>37</b>	4	6	..
Temp. ....	17	..	22	28	26	24	19	15	15	14	..
Numbers .....	0	3	9	23	44	21	28	<b>30</b>	2	1	0
Temp. ....	15	18	20	28	29	27	14	12	12	11	..
Numbers .....	1	2	33	54	72	37	6	<b>21</b>	0	0	0
Temp. ....	13	16	24	25	24	23	17	10	10	10	..
Numbers .....	0	1	28	40	30	19	5	<b>4</b>	0	0	0
Temp. ....	11	17	22	31	30	23	16	8	5	4	..
Mean numbers .....	0.4	10	33	55	54	34	10	<b>20</b>	4	31	2
Mean temperature ....	13	17	24	31	30	23	17	12	12	11	..
Maximum = 100 .....	0.7	18	60	100	98	62	18	36	7	5	..

The force and direction of the wind were also measured, and observations of the clouds made. Observations of the humidity of the air were made, but as the species flies in the brightest sunshine, low relative air humidity does not seem to play so important a part as in the case of other noctuids.

The results of the counts show that *P. gamma* has a very characteristic diurnal activity cycle (Table II and fig. 3 a). The average activity curve follows the temperature so that a peak is reached from noon to 2 p. m. at  $30^{\circ}$  C.<sup>1</sup>

<sup>1</sup> It is evident that if the counts had been taken later in the year when the temperature was lower, the peak would have been at a lower temperature. But as the counts were taken in the animals' optimal season, they have more than accidental value.

Activity then declined until 6 p. m., but after this there is a new rise at sunset (cp. WAHLGREN 1928, p. 248), and then the activity drops and remains low all night. Apart from the dusk observations, fig. 3 c shows a very clear correspondence between temperature and activity.<sup>1</sup>

The activity pattern is complex and variable because temperature and light, which rise and fall roughly together in nature, have in themselves opposite effects on activity, and because *P. gamma* unlike other noctuids is not immobilised by light. The curve registered is the activity pattern of feeding moths. This curve showing that the activity depends on two factors of which first one and then the other is the master factor, closely resembles the activity curve of *Hydroecia nictitans* Bkh. as recorded at Tipperne in 1941 and 1942 (fig. 3 b). As a rule this species seldom flies during the day and is chiefly active at night. If, however, bad weather sets in during the nights, the species is active in the daytime (presumably driven by hunger), and a midday feeding activity peak develops in addition to the evening one. Once the animal's light inhibition has been weakened, temperature becomes the "master factor", and a peak appears at the time of highest temperature, midday.<sup>2</sup> Later in the day the temperature falls and the activity is lowered as both temperature and light are unfavourable. Soon after sunset the light is favourable and becomes the master factor which outweighs the unfavourable influence of the falling temperature, and activity again increases. If there is a further drop in temperature, this outweighs the accelerating influence of the dark, and activity decreases. If, however, the night is favourable, the activity rises as shown in fig. 3 b (cp. LARSEN 1943, p. 372). A preference for activity in the dark must be presupposed in *P. gamma* if the curves of the two species are truly comparable, and the following section provides evidence that such a preference exists (p. 17).

The typical feeding behaviour of *P. gamma* was as follows: In the morning when temperature was low, there was no ac-

<sup>1</sup> VEIKKO (1946) argues the various flying periods may be due to differences of behaviour in the two generations.

<sup>2</sup> The possibility cannot be ignored that a diurnal cycle of nectar secretion by *Tanacetum* may affect the activity of *Hydroecia nictitans* (BOËTIUS 1948).



Fig. 4. *Plusia gamma* fluttering over heather. (E. B. L. fot.)

tivity. When the temperature in the sun rose to  $15^{\circ}$ – $20^{\circ}$  C. (measured immediately above the heather), the insects flew, but avoided the shade. If the weather was clear, activity increased very quickly (Table II,  $12/8$ ), but more slowly if it was rainy or cloudy (Table II,  $14/8$ ,  $15/8$ ,  $16/8$ ). During the first hour the temperature appeared to be too low to release the feeding reflex itself. Many of the moths did not feed but flew about at random, now and then basking in the sun for 10, 15, or 30 minutes (cp. KENNEDY 1939, p. 464). At noon all the insects were feeding actively, swarming over

the heather (fig. 4). Feeding activity then declined with the declining temperature.

About sunset and immediately after dusk the insects reappeared, feeding but also making sudden darting flights and seeming very restless. Soon they disappeared from the feeding stations near the ground and were found high up in the air, no longer feeding. FISHER (1938, p. 242) mentions that ATKIN and NEWMAN saw *P. gamma* rise from a field at dusk. The evening was stated

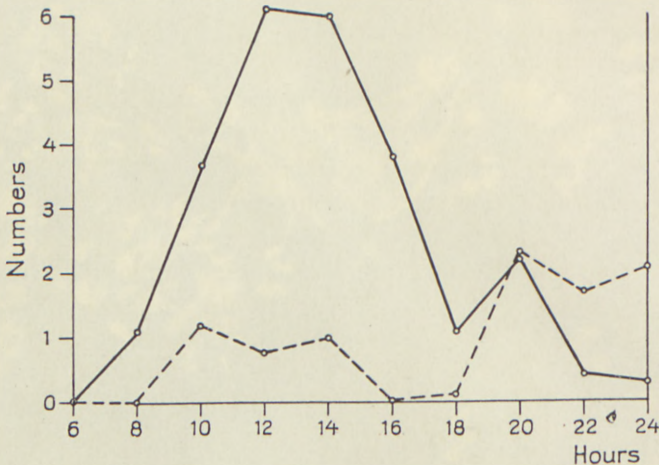


Fig. 5. Distribution of *Plusia gamma* on the stations. — Stations I—IX.  
--- Station II.

to have been warm and calm, and in one instance the insects flew straight upwards so that the direction of the flight could not be determined. FISHER believes this to have been the start of a migratory flight; in my opinion, however, the phenomenon observed by me—and by FISHER as well—is not the beginning of a directive migration, but is an expression of a migratory urge.

At station no. II the numbers of *P. gamma* were small during the day but much larger than at the other stations during the evening, when the temperature approaches the lower threshold value (cp. Table III and fig. 5). This was due to the fact that the day temperature above the *Chamenerium angustifolium* was comparatively low because the flowers were overshadowed by trees which in the evening prevented the rapid loss of heat by radiation typical of the open field heather.

Table III.  
Average activity at stations I—IX compared with  
the activity at station II.

	6	8	10	12	14	16	18	20	22	24
St. I—IX ÷ II ..	0.04	1.1	3.7	6.1	6.0	3.8	1.1	2.2	0.4	0.3
St. II .....	0.0	0.0	1.2	0.8	1.0	0.0	0.1	2.3	1.7	2.1

It is also noteworthy that at the time when the insects made restless, darting flights over the heather—as described above—the temperature there was lower than at two metres above it (cp. fig. 3), while earlier in the day the opposite was the case. This restless flight may perhaps indicate a beginning migratory restlessness, but since the animals evidently demand a high temperature of their own to be able to fly, the intensified movement may be an attempt at keeping their body temperature at a certain level in spite of falling temperature of the environment. (At an air temperature of 13° C. the temperature in the interior of the animals was measured at 25°.) Finally the experiments show that transition from light to dark in itself has an accelerating influence on activity. In places with less radiation the feeding activity ceases much later, and in such places the evening feeding activity may even surpass that of the daytime (unpublished reports from Dr. E. PALMÉN, Finland, and Mr. N. L. WOLFF, civil engineer, Denmark). Observations in Copenhagen late in the year showed no daytime activity whatever, only feeding insects being seen for half an hour at dusk, an observation corresponding to the evening peak in August. Evidently the day temperature was now so low that it could not—as in summer—outweigh the inhibitory influence of daylight on the activity of the insects even though a restricted feeding time had made them hungry.

Finally, it appears from Table II that both the size of the evening maximum and the number of insects flying during the night depend on the temperature. If this fell below a certain minimum, there was no evening activity (for instance <sup>16</sup>/<sub>8</sub>, 1946) as in that case the accelerating influence of the dark could not outweigh the inhibitory influence of the fall in temperature.

#### IV. Activity of *Plusia gamma* under Controlled Conditions.

While few experiments have been made on the dependence of the activity of noctuids on temperature and light, many other insects have been investigated in this way. *Ptinus tectus* for example (BENTLEY, GUNN and EWER 1941, p. 188) showed a pronounced diurnal rhythm dependent on the light and reversible by reversing the periods of light and darkness. Some species,

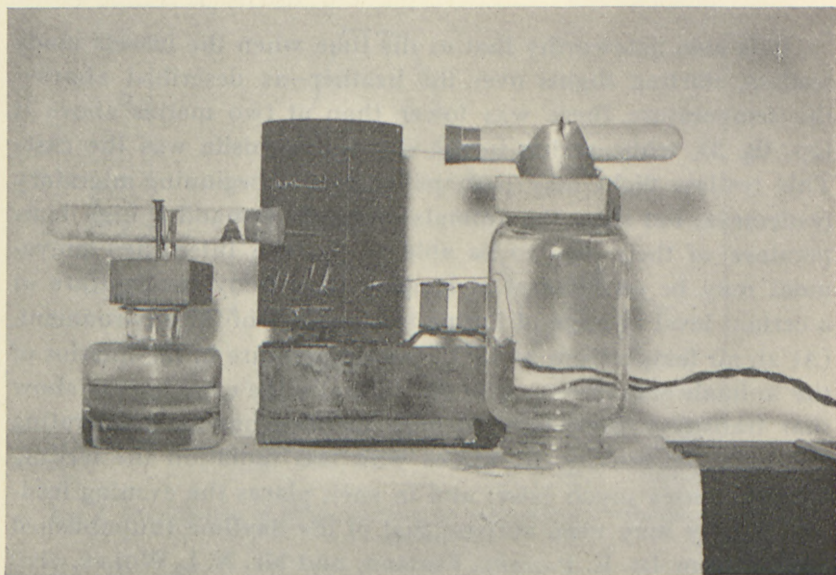


Fig. 6. The actograph. (E. Tetens Nielsen fot.)

for instance *Carambus pellucidus*, seem to be quite arrhythmic (PARK 1935, p. 165), while others—very few—seem to have a hereditary diurnal rhythm independent of light and darkness (*Megalodacne heros*, PARK 1935, p. 169). Sometimes we find a diurnal rhythm dependent on light but changing rather slowly when the light regime is changed, as for instance in the cockroach (MELLANBY 1940, p. 278, GUNN 1940, p. 267).

Individuals of *P. gamma* were tested in an actograph subjected to changes of light and temperature.<sup>1</sup> Individuals of

<sup>1</sup> The actograph was of a very simple design and quite adequate for the purpose. It consisted of a cellophane cylinder mounted on a rocking device with a stylus at one end writing on a smoked paper drum which rotated once every 24 hours (NIELSEN 1945, p. 75). (Fig. 6).

*P. gamma* were collected in July at the Mols laboratory and placed in the actograph. The insects were captured in sunshine and first exposed to a temperature of 19° C. They did not move, but when the temperature was raised to 22° C. during a quarter of an hour, they became very active for 5 minutes, and then quiet again. In another experiment with the test temperature between 19° and 20° C. for 5 hours *P. gamma* displayed no activity although individuals of the same species were very active in the field at the same time. The temperature was now increased to approx. 24° C., and the test animals became very active for a short time, to become quiet again afterwards. Similar experiments were repeated several times, and they all showed that at a temperature below 20° C. there was no spontaneous activity, whereas it was high at 22°-23°-24° C. One oviposition took place at 22.5° C. Later experiments with the August generation at Pilehuset showed some activity at 18°-20° C. (8 experiments), but it was twice as high at 21°-23° (6 experiments), whereas it did not increase correspondingly at still higher temperatures. The non-linear relation between activity and temperature over this part of the temperature range suggests that what occurs is not so much an evocation of activity by temperature, but rather a release of spontaneous activity at a temperature threshold of about 20° C.

Subsequent experiments were therefore made with a temperature of about 22° C. and a constant humidity. As a rule the test animals were collected from among those feeding outdoors at the evening maximum. Each experiment on *P. gamma* was duplicated with other noctuids. The insects were not fed during an experiment. Typical results were as follows:

I. (2 experiments). With darkness from 12 p. m. to 11. a. m. and light from 11 a. m. to 10 p. m. *P. gamma* showed moderate activity both in light and darkness, while *Amphipyra tragopoginis* only showed activity in darkness and when it was night outdoors (fig. 7).

II. (4 experiments.) When the order was reversed with light from midnight to 11. a. m. and darkness from 11 a. m. to 10 p. m., *P. gamma* was active both in the light and the dark, while *Agrotis c-nigrum* was active by day in the dark only (fig. 8).

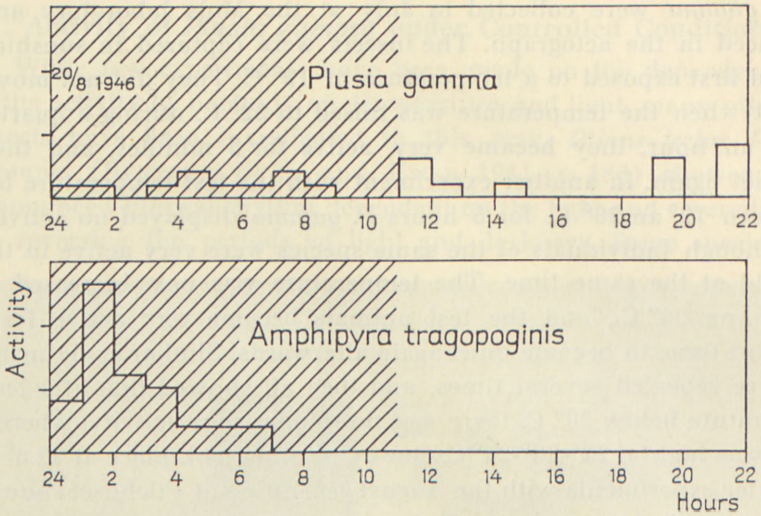


Fig. 7. Actograph experiments with *Plusia gamma* and *Amphipyra tragopoginis*. Shaded part = darkness. The abscissa shows in millimetres the part which is unblackened, when the writer scratches the roll as a consequence of the activity. See text.

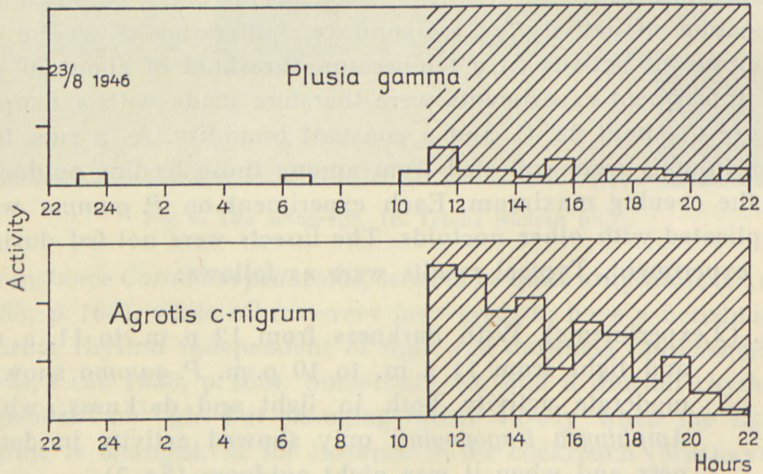


Fig. 8. Actograph experiments with *Plusia gamma* and *Agrotis c-nigrum*. See fig. 7.

III. (5 experiments). When exposed to constant light *P. gamma* showed sporadic activity both by day and by night while *Amphipyra tragopoginis* was inactive (fig. 9).



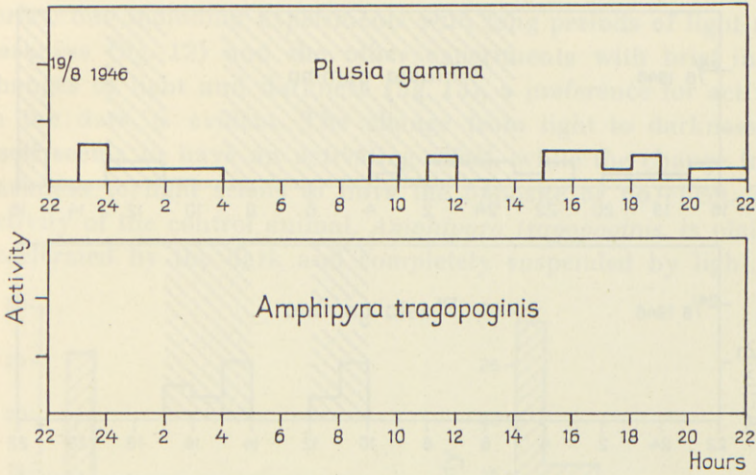


Fig. 9. Actograph experiment with *Plusia gamma* and *Amphipyra tragopoginis*. Light day and night. See fig. 7.

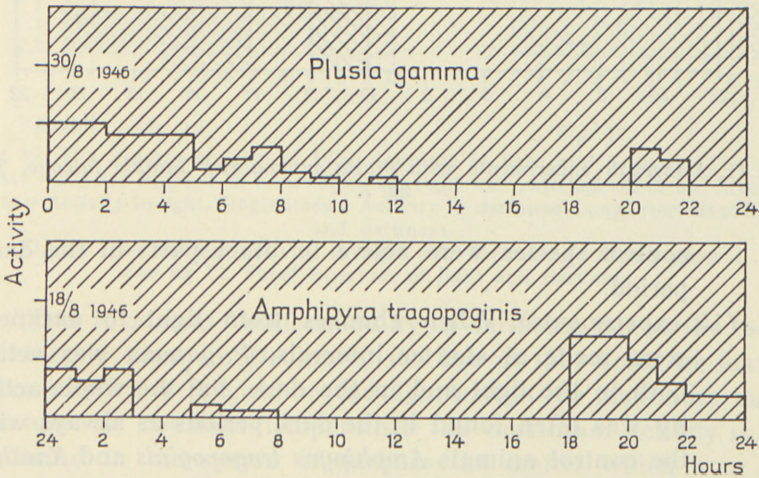


Fig. 10. Actograph experiments with *Plusia gamma* and *Amphipyra tragopoginis*. Darkness day and night. See fig. 7.

IV. (7 experiments). In complete darkness *P. gamma* was active during a considerable part of the 24 hours, while in this particular experiment *Amphipyra tragopoginis* was active in the night, morning and evening, but inactive in the middle of the day (fig. 10). In other experiments the

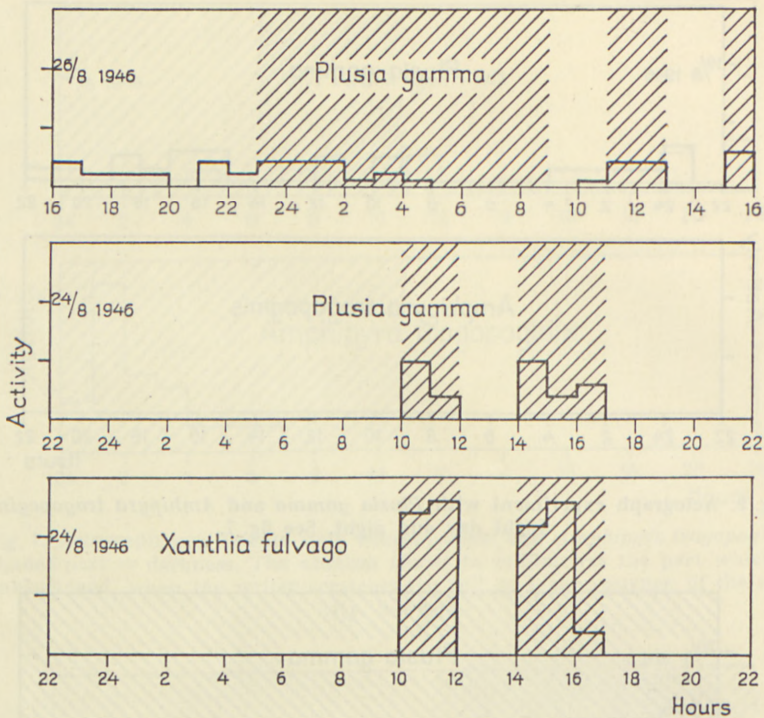


Fig. 11. Actograph experiments with *Plusia gamma* and *Xanthia fulvago*. See fig. 7.

control species were active in other parts of the dark period.

- V. (15. experiments). When changes from light to darkness were made at shorter intervals, *P. gamma* was active both in the light and in the dark, but the whole activity was often found in the dark periods as always with the control animals *Amphipyra tragopoginis* and *Xanthia fulvago* (fig. 11).

The sample experiments described above support the supposition of near indifference in *P. gamma* to light and darkness and to the hour of day. The noctuids used for control purposes showed a pronounced rhythm which was associated with light and reversible by it.

If, however, all experiments are gathered together in two

series, one including experiments with long periods of light and darkness (fig. 12) and the other experiments with brief interchanges of light and darkness (fig. 13), a preference for activity in the dark is evident. The change from light to darkness in itself seems to have an activating effect, while the change from darkness to light seems to have the opposite or no effect. The activity of the control animal, *Amphipyra tragopoginis*, is plainly accelerated by the dark and completely suspended by light.

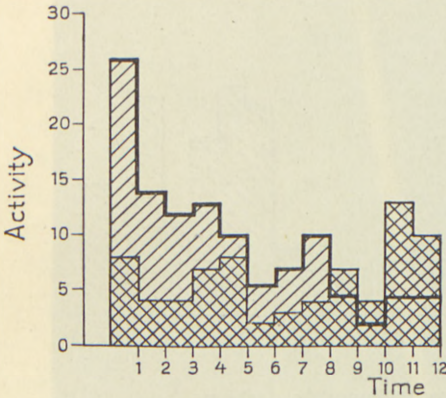


Fig. 12.

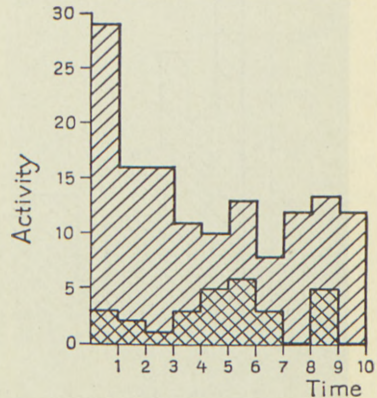


Fig. 13.

Fig. 12. The average activity of *Plusia gamma* in light and darkness. The Abscissa indicates number of hours since the light was switched off or on. Crossed lines = Activity in light, Single lines = Activity in darkness. Long intervals of light and darkness.

Fig. 13. The average activity in light and darkness of *Plusia gamma*. See fig. 12. Short intervals of light and darkness.

Thus *P. gamma* "prefers" to fly in darkness, but as the temperature is often (in Denmark) too low at that time, the maximum activity is reached in the light and at the maximum temperature. At constant temperature the maximum activity is to be found in the period of darkness no matter which hour of the day this is.

When the activity of individuals kept in darkness was recorded (the test animals were unfed and used for only 24 hours; five experiments were made) the average values shown in fig. 14 were obtained.

On the assumption that this activity pattern is not accidental, the curve may be interpreted in the following way: The peak just after midnight is caused by the onset of darkness

when the experiment begins, the animals having been in artificial light before that. Then there is a decrease of activity corresponding with that observed under natural conditions. With a constant temperature there is no increase towards noon. The insects normally feed at noon and may therefore be supposed to feel hungry at that time, but as normally accompanying factors such as rising temperature, sunshine, scent of

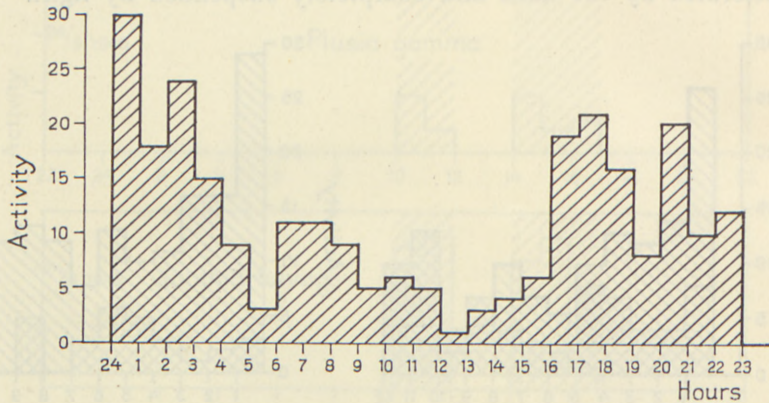


Fig. 14. Average activity in complete darkness.

flowers, etc., are absent, the feeding activity is postponed, expressed by the activity from 16—22 in fig. 14.

### V. The Migratory Flights.

The preference for activity in dim light already mentioned combined with the need for a high temperature explain the two peaks of the activity curve obtained in the field, but this of course, was for feeding activity only (cp. p. 10). Although feeding activity ceases about 9 p. m. at the stations, flying does not. It is by now too cold for flight near the ground, but the insects rise as temperature inversion proceeds and continue flying in the warmer air aloft for some hours (cp. p. 21). Now *P. gamma* is a well-known migrant and this high-flying, non-feeding phase of their diurnal behaviour is one that could readily involve long-range movement. Of course many other noctuids will be seen simultaneously in the air, and also some at a similar

height, but their normal behaviour differs from that of *P. gamma* in various respects.

(1) *P. gamma*'s flight differs from the feeding flight in being drifting, floating and "unenergetic", while other noctuids fly about fast and energetically. (2) *P. gamma* does not seek food



Fig. 15. The projector put on. (E. Tetens Nielsen fot.)

and flies downwind, while other noctuids most often go against the wind following the smell drifts from the food (nectar) or the opposite sex. (3) The two sexes are represented in a way differing from "normal" noctuids caught by light. In noctuids the males generally preponderate very considerably in light catches; WILLIAMS (1936) found the males constituting 81 %, DERCKS (1939) 77 %, and WILLIAMS (1939) 83 %; in the observation period from Pilehuset, touched upon, the light catch showed 72 % of males. In *P. gamma* the male-percentage, however, only was  $44 \% \pm 3.7 \%$ , and this was not due to the fact that the females outnumbered the males in the population, since by day-counting on the heather the percentage of males was determined at  $55 \% \pm 1.9 \%$ . This means

that in the population males and females are present in almost equal numbers, and during the nights they fly in this proportion,<sup>1</sup> which seems to indicate that *P. gamma*'s night-flight has another function than that of the other noctuids, where feeding and copulation are the main problems, two functions in which the ♂♂ always are the most active (cp. HERING 1932). This flight are therefore here called migratory flight.

The high-flying nocturnal activity of the insects was observed in the beam of a searchlight (fig. 15). The light can be revolved so that the individual flight may be observed.

High-level flying began shortly after the heather-level activity had passed its evening maximum; it increased until about midnight, and then it decreased until ceasing at 2 p. m. The night activity depended on temperature and wind, being enhanced by high temperature and inhibited by strong wind. In table IV three grades of high-flying activity are distinguished<sup>2</sup>: (1) Nil, (2) moderate, and (3) intense, according to the number of moths

Table IV.  
Correlation between combined factors and activity.

Date	Tcmp.	Wind	t—w	1	2	3
6/8.....	18°	1—2	16	..	..	x
7/8.....	17°	1—2	15	..	..	x
8/8.....	20°	0—1	19	..	..	x
10/8.....	18°	7	11	x	..	..
11/8.....	14°	5	11	..	x	..
12/8.....	17°	5	12	..	..	x
13/8.....	16°	8—9	7	x	..	..
14/8.....	13°	7	6	x	..	..
15/8.....	12°	0—1	11	x	..	..
16/8.....	11°	2	9	x	..	..
17/8.....	14°	1	13	..	..	x
19/8.....	16°	0—1	15	..	..	x
21/8.....	13°	0—1	12	..	x	..
22/8.....	15°	2	13	..	x	..

<sup>1</sup> In a few other species equal numbers of ♂♂ and ♀♀ can be observed, too; especially towards the end of the activity period of the species the ♂—percentage will go down, because noctuids are prothandric.

<sup>2</sup> It is to be regretted that only three categories could be set up; but exact counts were only taken during some nights of observation as the influence of the physical factors on the migration had not been taken into account.

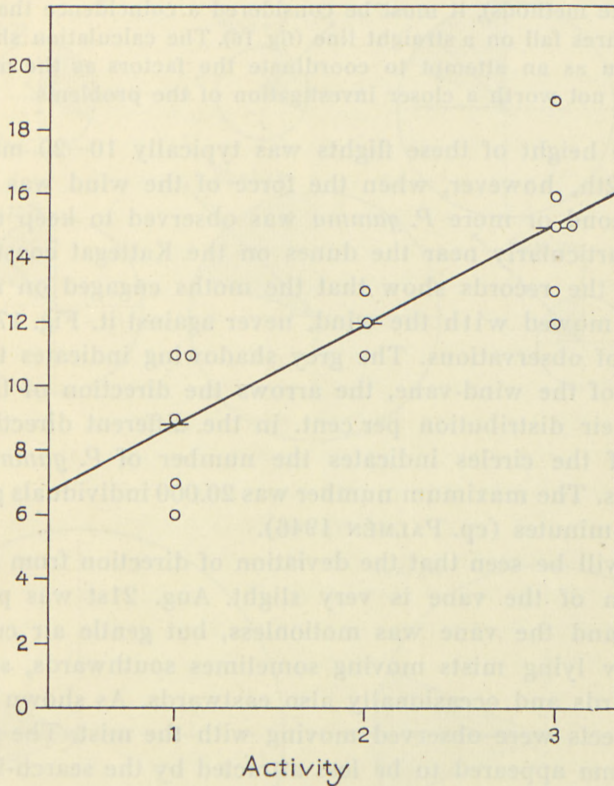


Fig. 16. Correlation between activity and combined climatic factors for *Plusia gamma*. The Abscissae shows the three grades of activity, the ordinate the difference between the temperature and the strength of the wind blowing at the same time ( $t-w$ ) See text. The graph has been drawn through the average values.

observed. Table IV shows no correlation between activity and temperature alone or wind alone (cp. LARSEN 1943, p. 358, 363), but the activity depends upon both these factors.

If we try to combine the activating influence of temperature with the inhibitory influence of increasing wind, by assuming that activity rises in a nearly straight line with rising temperature, over the temperature range in question and falls in a straight line with increasing wind force, over the range of wind forces in question, then the combination will be  $t-w = \text{activity}$ . This is done in Table IV, from which it appears that high values of  $t-w$  coincide with intense activity, whereas there is no activity when the combination of both factors falls below 11. With so rough a method of recording activity and of combining the effects of temperature and wind (the material does not deserve more

elaborate methods), it must be considered a coincidence that the average figures fall on a straight line (fig. 16). The calculation should only be taken as an attempt to coordinate the factors as the material at hand is not worth a closer investigation of the problems.

The height of these flights was typically 10–20 metres. On Aug. 12th, however, when the force of the wind was 5 metres per second or more *P. gamma* was observed to keep unusually low, particularly near the dunes on the Kattegat coast.

All the records show that the moths engaged on migratory flights mowed with the wind, never against it. Fig. 17 shows a series of observations. The grey shadowing indicates the movements of the wind-vane, the arrows the direction of the flights and their distribution per cent. in the different directions. The area of the circles indicates the number of *P. gamma* per 10 minutes. The maximum number was 20.000 individuals per 100 m in ten minutes (cp. PALMÉN 1946).

It will be seen that the deviation of direction from the mean position of the vane is very slight. Aug. 21st was practically calm, and the vane was motionless, but gentle air current set the low lying mists moving sometimes southwards, sometimes westwards and occasionally also eastwards. As shown in fig. 17 the insects were observed moving with the mist. The migrating *P. gamma* appeared to be less attracted by the search-light than other noctuids, but as they greatly outnumbered the latter, many specimens were secured all the same.

It was hardly possible to distinguish in what direction the insects were facing and therefore flying (their "courses"—see GUNN et al., 1948), and these records refer only to their "tracks", i. e. the directions in which they were moving over the ground, the resultant of their own flight exertions and the movement of their medium, the air.

Exact measurements of the ground speed of the migrants would have helped to determine how far the insects on the one hand and the wind on the other, were responsible for the speed and direction of the insects relative to the ground.

The outstanding point is that the tracks of the moths were always down-wind, so that any long-range movements occurring during this migratory flying would also be with the wind.



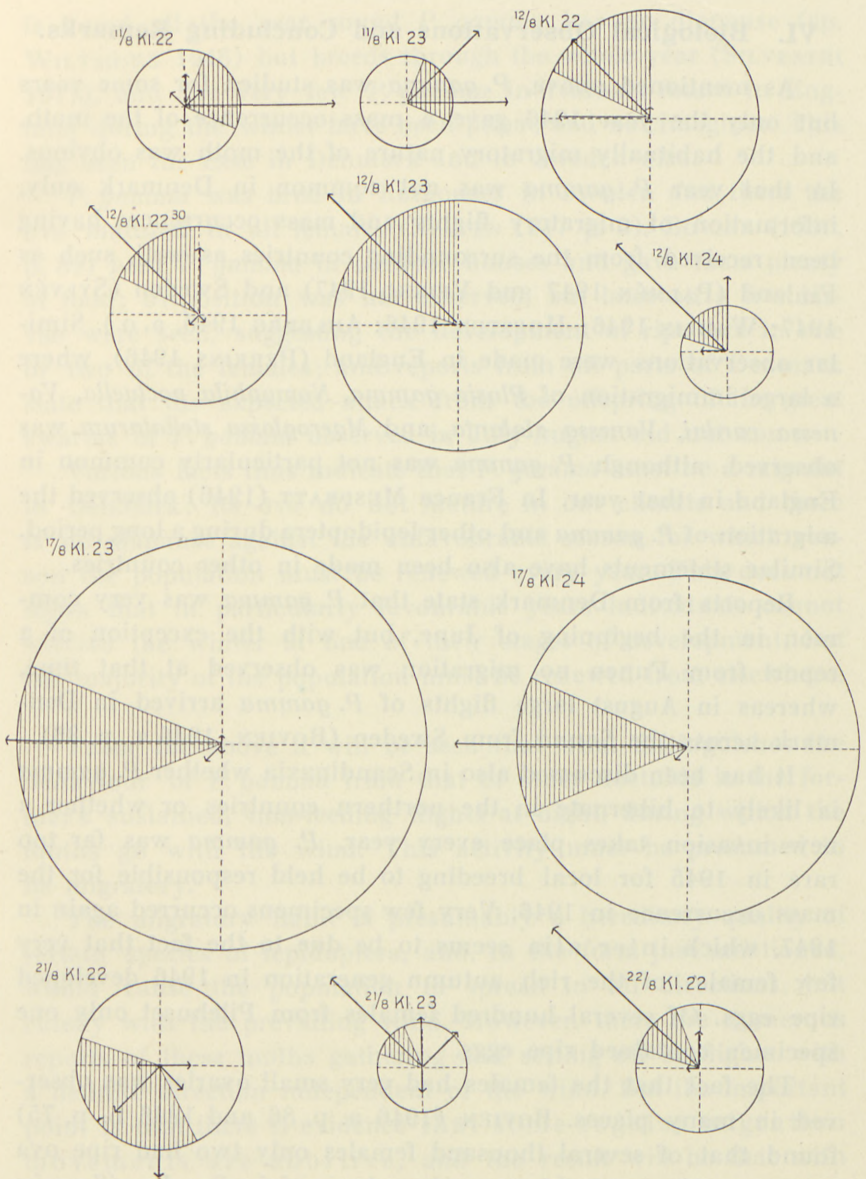


Fig. 17. Diagram of flying direction, direction of wind (shaded areas), and grade of activity. The arrows show the direction of flight and their length indicate the percentage distribution of the animals in various directions. The size of the circles indicates the number of animals observed. Kl. = o'clock.

## VI. Biological Observations and Concluding Remarks.

As mentioned above, *P. gamma* was studied for some years but only the year 1946 gave a mass occurrence of the moth, and the habitually migratory nature of the moth was obvious. In that year *P. gamma* was not common in Denmark only, information of migratory flights and mass occurrences having been received from the surrounding countries as well, such as Finland (PALMÉN 1947 and VEIKKO 1947) and Sweden (SYLVÉN 1947; WAHLIN 1946; HOFSTEN 1946; AHLBERG 1946, a. o.). Similar observations were made in England (PERKINS 1946), where a large immigration of *Plusia gamma*, *Nomophila noctuella*, *Vanessa cardui*, *Vanessa atalanta*, and *Macroglossa stellatarum* was observed, although *P. gamma* was not particularly common in England in that year. In France MUSPRATT (1946) observed the migration of *P. gamma* and other lepidoptera during a long period. Similar statements have also been made in other countries.

Reports from Denmark state that *P. gamma* was very common in the beginning of June, but with the exception of a report from Funen no migration was observed at that time, whereas in August large flights of *P. gamma* arrived in Denmark across the Sound from Sweden (BOVIEN, 1946 a, p. 86).

It has been discussed also in Scandinavia whether *P. gamma* is likely to hibernate in the northern countries or whether a new invasion takes place every year. *P. gamma* was far too rare in 1945 for local breeding to be held responsible for the mass occurrence in 1946. Very few specimens occurred again in 1947, which inter alia seems to be due to the fact that very few females of the rich autumn generation in 1946 developed ripe eggs. Of several hundred females from Pilehuset only one specimen contained ripe eggs.

The fact that the females had very small ovaries was observed in many places. BOVIEN (1946 a. p. 86 and 1946 b. p. 75) found that of several thousand females only two had ripe ova in the ovaries, and this was also observed in Sweden (SYLVÉN 1947 p. 10). FISHER (1938 p. 232) mentions from England that all females of *P. gamma* sent to her had undeveloped ova and small ovaries. Hence she concludes that *P. gamma* hibernates as imago. However, it seems that in places where the species

is found all the year round *P. gamma* has no diapause (cp. WILTSHIRE 1946) but breeds through the whole year (SILVESTRI 1911), and the very few *P. gamma* individuals found in England during the winter have been pupae and not imagines. This has been the case in Denmark and in Sweden also.

*P. gamma* was bred in hothouses in Sweden and there the ova matured in all females (SYLVÉN 1947 p. 9). BOVIEN (1946, p. 89) bred *P. gamma* in outdoor houses and gave them plenty of food; oviposition was not observed, but later on a few larvae were seen, suggesting the development of ripe ova in one or two of the females; and reports from all parts of Denmark state that the expected attack from the offspring of the great swarms of *P. gamma* observed in July-August did not come.

Various facts thus indicate that *P. gamma* must be a migrant in Denmark: Its ova do not mature in our climate and there is no diapause against the unfavourable season for which reason the population must be renewed every year. This does not mean that in particularly favourable years individuals cannot survive the winter at one of their stages of development, but the majority of the population must be renewed from elsewhere.

From the above it will be seen that what distinguishes the behaviour of *P. gamma* from that of other noctuids is the former's sustained, non-feeding flights at night, during which the moths go with the wind. This activity must be presumed to be migratory.

The migratory habit is presumably a hereditary quality of certain species of lepidoptera, and, in the form just mentioned, would cause the population to spread in all directions, but chiefly with the prevailing wind. However, there are numerous reports of these moths gathering and setting off in flights with a definite direction independent of the wind. But the important point is that there is evidence that some regular migration movements are abortive, and the result will be that with variable winds parts of the populations will largely keep within a limited but large area, and that the gradual elimination of the migratory habit which according to WILLIAMS should take place at the centre of the outbreak (WILLIAMS 1942, p. 250) need not occur even if migrations with definite orientation take

place. Thus, a return flight is not necessary for maintaining the migratory tendency of the species (cp. WILTSHIRE 1946).

The migrations of *P. gamma* have been compared with the regular migrations of birds, northwards in the spring and southwards in the autumn (FISHER 1938). In the author's opinion, however, the comparison is not quite satisfactory because *P. gamma* breeds more freely in the south than in the north all the year round. Nor has it a diapause in the south, so a northward migration would seem valueless

Even with no self-determined direction of the migratory flight it will be seen that *P. gamma* in places like England, where it does not occur in winter, will come from the south where it is notoriously found in the winter, and this circumstance may be taken into consideration when its disappearance in the autumn is to be explained: From each locality the insects spread in the direction of the prevailing winds, but on account of the reduced activity in colder regions the north-bound insects will be less noticeable and will die earlier on account of the lower temperature. But of course this does not disprove a return flight.

Large migratory flights of *P. gamma* will often, at least when observed from the same place, be seen moving in the same direction, independently of variations in wind and light, for a long period. For the formation of such migratory flights more than an increased activity is needed, namely the development of gregarious behaviour. That this is present in *P. gamma* has been, if not proved, at least suggested by the following statement. Mr. HENNING ANTHON (unpublished) observed in fields of flowering clover where the insects were swarming in dense crowds, that excitation centres occasionally sprang up which spread in an undulating manner so that waves of insects set off together. Often they flew only for a short time before they landed again, but all the same the observations seem to indicate that gregarious behaviour does occur. If, then, the insects did not land again, there would be considerable "gregarious inertia" over a wide starting front, which would enable the whole flight to keep to the same direction for some time (cp. KENNEDY 1945, p. 252).

The vision of *P. gamma* is excellent, and the swarm might

well keep together by the individuals making compensatory reactions to one another and, from time to time, to the sun (cp. KENNEDY 1945, p. 256). Their hearing is also exceptionally keen<sup>1</sup> and may help to keep the flight together in darkness.

### Acknowledgements.

I am highly indebted to Dr. H. M. THAMDRUP, Director of the Mols laboratory, and to Dr. E. TETENS NIELSEN, Director of the laboratory of Pilehuset, for their great hospitality and help.

Grateful acknowledgement is made to Mrs. AASE HOLST who has undertaken the translation of this paper into English, and to Dr. J. S. KENNEDY for his helpful criticism and corrections of the M. S.

Copenhagen, Nov. 25th 1948.

### Summary.

(1) Parallel field observations and laboratory experiments were made on *Plusia gamma* in Denmark, particularly during its mass appearance in 1946, in an attempt to analyse its behaviour and phenology in comparison with other, non-migrant noctuids.

(2) The preferred temperature of *P. gamma* was determined experimentally as 25–30° C., considerable higher than that of other noctuids active in the same season. Its activity was negligible below 18–20° C.

(3) *P. gamma* was active in the laboratory both in light and darkness and regardless of the time of day, whereas the other species were active only in the dark. But *P. gamma* showed a preference for activity in the dark and was especially responsive to a change from light to darkness.

(4) In the field, *P. gamma*'s feeding activity showed two peaks: a temperature-dependent one at midday and a light-dependent one at dusk, which contrasts with the typical noctuid

<sup>1</sup> It is almost impossible to photograph the insects with a reflex camera because the slight noise caused by the turning of the mirror puts them to flight.

curve with its night peaks. Where trees or cloud cover delayed the cooling of the ground the night peak sometimes surpassed the midday one and feeding continued far into the night. In the absence of such cover the night peak was smaller than the midday one and feeding decreased rapidly with falling temperature after dark.

(5) When evening temperature inversion occurred and feeding activity ceased the moths rose into the upper, warmer air layers, where they continued flying till after midnight. The moths always moved in the same direction as the wind during this high-level, non-feeding flight activity, which is regarded as migratory.

(6) The failure of *P. gamma*'s ova to mature in Denmark, its lack of diapause and its high preferred temperature, show that its home must be elsewhere in a warmer climate, whence the Danish population must be replenished every year. Its exceptional readiness to feed in the daytime enables it to exist in cooler regions, covering a far wider geographical range, than other noctuids with a similar temperature preference. Its migratory tendencies enable it to reach these regions, but some of its most regular journeys, as to Denmark, may be quite "abortive" for the insects concerned.

---

## Literature.

1. AHLBERG, H. 1946. Gamma flyet 1946. Växtskyddsnotiser Nr. 6.
2. BENTLEY, E. W., GUNN, D. L. and EWER, D. W. 1941. Biology and Behaviour of *Ptinus tectus* Boie. L. The Daily Rhythm of Locomotory Activity Especially in Relation to Light and Temperature. Journ. Exp. Biol. Vol. XVIII.
3. BOËTIUS, J., 1948. Über den Verlauf der Nectarabsonderung einiger Blütenpflanzen. Beih. Schweiz. Bienen-Z. B. 2 H. 17.
4. BOVIEN, P. 1946 a. Gammauglens Masseoptræden i 1946. Naturhistorisk Tidende Nr. 6.
5. — 1946 b. Maanedsoversigt over Plantesygdomme 285 and 287.
6. FISHER, K. J. 1938. Migrations of the Silver-Moth (*Plusia gamma*) in Great Britain. Journ. Animal Ecol. 7.
7. FRAENKEL, G. 1932. Die Wanderungen der Insekten. Ergebn. der Biol. IX.
8. GUNN, D. L. 1940. The Daily Rhythm of Activity of the Cockroach, *Blatta orientalis* L. II. Observations and Experiments on a Natural Infestation. Journ. Exp. Biol. 17.
9. — and others. 1948. Locust Control by Aircraft in Tanganyika.
10. HERING, M. 1926. Biologie der Schmetterlinge. Berlin.
11. HERTER, K. 1923. Untersuchungen über den Temperatursinn der Feuerwanze (*Pyrrhocoris opterus* L.). Biol. Zbl. 43. p. 27—30.
12. HOFSTEN, C. G. VON. 1946. Gammaflyets härjningar av betydanda omfattning. Några iakttagelser och reflexioner. Lantmannen Nr. 33.
13. KENNEDY, J. S. 1939. The Behaviour of the Desert Locust (*Schistocerca gregaria* Forsk.) in an Outbreak Centre. Trans. Roy. Ent. Soc. Lond. 189. o. 385—542.
14. — 1945. Observations on the Mass Migration of Desert Locust Hoppers. Trans. R. Ent. Soc. Lond. 95, 247.
15. LARSEN, ELLINOR BRO. 1943. The Importance of Master Factors for the Activity of Noctuids. Studies on the Activity of Insects I. Entomol. Medd. XXIII. Copenhagen.
16. — Quantitative Studies on the Activity of Noctuids. Studies on the Activity of Insects II. (In press).
17. MELLANBY, K. 1940. The daily Rhythm of Activity of the Cockroach, *Blatta orientalis* L. II. Observations and Experiments on a Natural Infestation. Journ. Exp. Biol. 17.

18. MUSPRATT, V. M. 1946. Migration of Lepidoptera at St. Jean/de Luz, Basses Pyrénées, in June, and in the Hautes Pyrénées June—July 1946. The Entomologist. Vol. LXXIX.
19. NIELSEN, E. TETENS 1945. Moeurs de Bembex. Spolia zool. Mus. Havn. VII.
20. PALMÉN, E. 1947. Ein auffallender Massenflug von *Phytometra gamma* L. und *Pyrameis cardui* L. (Lep.) in Südfinland. Ann. Ent. Fenn.
21. PARK, ORLANDO, ROBERTS, T. W. and HARRIS, S. J. 1941. Preliminary Analyses of Activity of the Cave Crayfish *Cambarus pellucidus*. The Amer. Naturalist. Vol. LXXV.
22. PARK, ORLANDO and SEJBA, O. 1935. Studies in Nocturnal Ecology IV. *Megalodacne Heros*. Ecology. Vol. XVI. No 2.
23. PERKINS, R. C. L. 1946. *Sterrhia saeraria* L. (Lep.) and Other Immigrants near Lydford Devon. Ent. Monthly Mag. 4. Se. No. 83.
24. SILVESTRI, F. 1911. Contribuzioni alla conoscenza degli insetti dannosi e dei loro simbionti. II. *Plusia gamma* L. Boll. Labor. Zool. Gen. Agr. Vol. V.
25. SYLVÉN, E. 1947. Undersökningar över Gammaflyet, *Phytometra gamma* L. Statens Växtskyddsanstalt. Nr. 48.
26. WAHLGREN, E. 1928. Massupträdande af *Phytometra gamma* L. Entomol. Tidsskrift. Stockholm.
27. WAHLIN, B. 1946. Gammaflyets härjningar i Östergötland. Lantmannen Nr. 36.
28. WALOFF, Z. 1946. Seasonal Breeding and Migrations of the Desert Locust in Eastern Africa. Anti-Locust Memoir I. London.
29. VEIKKO, K. 1947. Über das Massenaufreten der Gammaeule, *Phytometra gamma* L. (Lep. Noctuidae) im Sommer 1946 in Finland. Ann. Entomologici Fennici. Nr. 3.
30. WILLIAMS, C. B. 1930. Migrations of Butterflies. Edinburgh.
31. — 1935. The Times of Activity of Certain Nocturnal Insects chiefly Lepidoptera as Indicated by a Light Trap. Trans. R. Ent. Soc. Lond. 83.
32. — 1939. An Analysis of Four Years Captures of Insects in a Light Trap. Trans. R. Ent. Soc. Lond. 89.
33. — G. F. COCKBILL, and GIBBS, M. E. 1942. Studies in the Migration of Lepidoptera. Trans. R. Ent. Soc. Lond. 92.
34. WILTSHIRE, E. P. 1946. Studies in the Geography of Lepidoptera III. Trans. Roy. Ent. Soc. Lond. Vol. 96.