23.

The Importance of Master Factors for the Activity of Noctuids.

Studies on the activity of insects I.

By

Ellinor Bro Larsen.

The present paper records parts of a series of investigations on the activity of the Noctuids made by the author in the period 1937—42. In 1938 and 1939 I worked in collaboration with Dr. E. Tetens Nielsen in the laboratory Pilehuset, whence important sections of the investigation are derived. The rest of the investigation was made in the laboratory of Tipperne, supplemented by investigations carried out in the laboratory of Skallingen. In the succeeding pages some of the results of these comprehensive investigations will be presented in order to illustrate the activity of the Noctuids considered from the point of view of the influence of master factors.

It is well known, i. a. from animal geography (Hesse 1924[1]), that the factors most frequently lying about the minimum demands of a species determine the distribution of the animal. As regards plants, Liebig[1]) has previously demonstrated that the nutritive substance most sparsely present determines the thriving of the plant, and my object in the following pages is to show that the activity of insects, also, is subject to the influence of master factors, which should be taken to mean that the activity is governed by the factor which for the time being lies at about the minimum demand of the species.

Since only a combination of a limited number of factors is dealt with below, viz. those assumed by the author to be of the greatest importance, the dependence is only given in broad features, and deviations in individual observations will frequently be noted. Some few species do not follow the main rules which

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1) Hesse, R. Tiergeographie auf ökologischer Grundlage, 1924, p. 17.

apply to the dominating species of the particular stock; in a few cases only the conditions of some species are pointed out in order to illustrate a wider interdependence.

In recent years a series of laboratory experiments notably in practical entomology has been made in order to determine the optimum conditions and the border values for the resistance of a number of species to physical factors, i. a. so as to be able to predict something about the extent and occurrence of impending insect pests. However, it is often difficult to find complete agreement between the results of the laboratory experiments and the observations in nature, where we are concerned with an interaction of the physical factors. A fact rendering the conditions even more complicated is that the deviations from the experimental data for the same species appear now in one now in another field.

I think that the cause of such disagreements — at any rate as regards the Noctuids — often is that now one now another factor approaches the minimum demand and accordingly comes to dominate the other factors.

Technique and Test Animals.

The activity of the Noctuids was chosen as the subject because it takes place by night and it was thus possible to avoid the direct effect of the sun's rays and the insolation associated with it — factors which are of great inportance but are difficult to measure. The Noctuids were chosen as test animals, because their systematics and biology were known to me beforehand, and during flight they are exposed to the physical factors under such conditions that it is possible to measure these factors.

The detailed planning of the investigation and the technique employed have been explained in another paper[1]); here it need only be pointed out:

1) that the activity has been investigated in relation to the factor hunger; accordingly nothing can be stated about other sorts of activity.

2) Boxes of uniform size were arranged in suitable places of the terrain and were covered with a sugar bate every evening to attract the animals.

3) The activity of the species may then be measured by counting, at certain intervals in the course of twenty-four hours, the

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1) Quantitative Studies on the Activity of Noctuids. Studies on the Activity of Insects II. Ellinor Bro Larsen and E. Tetens Nielsen (in press).

number of individuals present on the boxes; at the same time various physical factors assumed to be of importance for the activity are measured, for instance the light intensity, humidity of the air, temperature, force of wind, and precipitation.

The chief biological source of discrepancies is that the size of the population is unknown and constantly changes owing to emergence of fresh animals. A consequence of this is seen in Fig. 5, where the intensity of the activity follows the temperature for a number of nights, but increases excessively from August 2nd, though the temperature remains nearly constant; this took place, because an almost explosive emergence of the dominating species *Amphipyra tragopoginis* set in. Another source of error is that the population includes species of widely different physical demands, and this makes itself especially felt in the transitional periods, spring and autumn, when the spring stock is replaced by the summer stock, and the summer stock by the autumn stock (cf. Fig. 8).

4) Finally it should be mentioned that in the majority of the twenty-four hour curves the maximum number of animals is stated to be 100 and the numbers of the other counts have been computed in proportion to this; thus it is possible to compare the distribution on nights with few animals and on such with many animals.

Light as a Master Factor.

It is hunger that induces the Noctuids to approach the boxes with food, but twenty-four hour counts show that the approach of the animals to the boxes is not equally distributed over all the hours of the day and night; thus it will be seen from Fig. 1, a that in the first half of July the Noctuids only fly from about 9 p. m. to 3 a. m. The cause of this may be that a regular inherited rhythm is induced in the animals, or that at certain times of the twenty-four hours the light is a master factor and governs their activity. In order to test whether the first of these alternatives holds good, specimens of *Agrotis pronuba,* the most frequent species in the series Fig. 1, a, were placed in an activograph in a light-tight thermostat. It turned out that if day and night are exchanged, so that it is light from 10 p. m.

to 10 a. m. and dark from 10 a. m. to 10 p. m., a slight activity may be noted at 9 p. m. during the first days, that is to say, at the time the activity normally takes place; but it ceases when the light is lit at 10 p. m.; the most intense activity, however, occurs immediately after the light has been put out at 10 a. m., and after a couple of days the whole activity occurs after 10 a. m. Thus there is a small tendency to a rhythm, but the

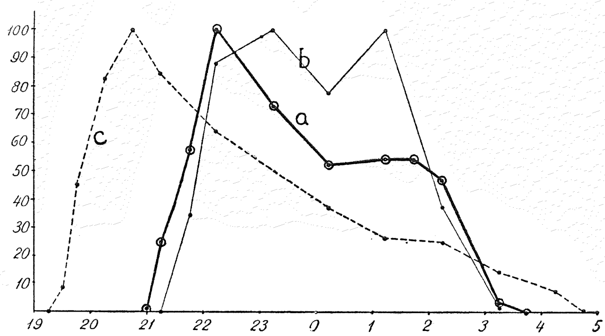

Fig. 1. The twenty-four hour activity at three different seasons, a —— July 1939, b —— June 1940, and c ---- September 1939. Ordinate: number of individuals in percent of the maximum number; abscissa: hour. — a and c: Pilehuset, b: Tipperne.

influence of light will soon make itself felt and eliminate the rhythm.

That the influence of the light determines the activity will also appear from observations made in nature. Thus a comparison of a, b, and c in Fig. 1 will show that the activity does not always occur from 9 p. m. to 3 a. m., but in the light month of June it sets in later and ceases earlier than in the darker September. (Roughly the activity sets in when the colours disappear to the human eye, and ceases when colours can again be distinguished in the landscape).

According to the above we may conclude that the impulse of the activity is, indeed, the sensation of hunger, but when the intensity of the light increases, it will "sink" below the minimum demand of the species and impede the activity — in July before 9 p. m. and after 3 a. m. in every twenty-four hour period. If the intensity of the light ranges around the minimum demand, light becomes a master factor and determines

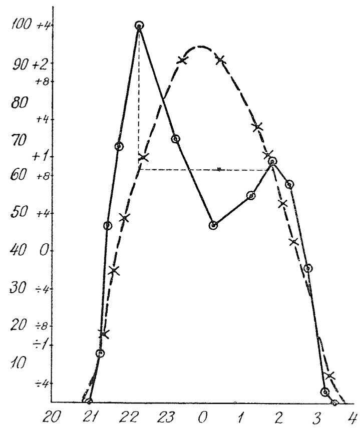

Fig. 2. Comparison between twenty-four hour activity and intensity of light. —— mean curve for nights with a two-peaked activity curve in the period $^4/_7$-$^{16}/_7$ 1939. –×– mean light curve for the same period. Abscissa: hour; ordinate, large figures: number of individuals in percent of the maximum number; small figures: log. sec. illumination. — Pilehuset.

when the activity sets in. Besides from the general normal twenty-four hour curve, this is seen i. a. from the fact that in a dark overcast evening the activity sets in about half an hour earlier than in a clear evening, and Noctuids kept in a laboratory will begin to fly earlier in the evening than those in the open, because the threshold value of the light intensity will be passed earlier indoors than out-of-doors.

From the curves Fig. 1, a and Fig. 1, b[1]) it will be

[1]) Fig. 1c is derived from nights with a late moon and therefore show different conditions.

seen that the activity is not equally intense throughout the period of activity; the liveliest activity occurs shortly after the beginning of the period, and another increase sets in shortly before the period ceases, the activity curve being accordingly two-peaked. Fig. 2 shows the light curve for July 1939, together with a mean curve of the two-peaked activity curves for the same period. They have the abscissa in common; as ordinate for the light curve has been used the time a photographic plate of a certain sensitiveness to light must be exposed at that particular light intensity. The ordinate is accordingly greatest at midnight, declining logarithmically towards both sides. It will be seen that the two peaks of the activity curve occur at about the same intensity of light[1]), in this case at about five seconds' exposure. That means that the light not only behaves as a master factor in every twenty-four hour period, but that a preferential light intensity, which favours the activity of the dominant species, is also present.

Temperature as a Master Factor.

If hunger and light were the only factors affecting the activity, it might be expected that the activity curve would be two-peaked every night[2]); however, Fig. 3 shows that on July 4th, 9th, 11th, and 16th there was no morning maximum, and on July 13th the curve after midnight was almost straight. Thus other factors must exert their influence, inhibiting the accelerating influence of the light. As the temperature was subject to fairly large fluctuations during the period, it was reasonable to correlate it with the phenomenon in question.

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[1]) It is true that the maximum number of animals was found at 1.45 a. m., but this is due to too few readings; the maximum occurs very near 2 a. m.

[2]) Nights with moonlight of course excepted.

Table I.

Date		0	1	2 Hour
$^{4}/_{7}$	1939	**12.3**	**13.1**	**13.7**
$^{5}/_{7}$	„	16.9	16.9	16.8
$^{7}/_{7}$	„	15.5	15.4	15.7
$^{8}/_{7}$	„	17.2	17.5	17.5
$^{9}/_{7}$	„	**10.5**	**11.7**	**11.6**
$^{10}/_{7}$	„	13.4	13.6	13.4
$^{11}/_{7}$	„	**11.7**	**11.6**	**11.9**
$^{13}/_{7}$	„	**12.7**	**11.9**	**12.8**
$^{14}/_{7}$	„	15.2	15.5	15.0
$^{15}/_{7}$	„	17.0	16.9	16.9
$^{16}/_{7}$	„	**12.8**	**12.4**	**11.8**

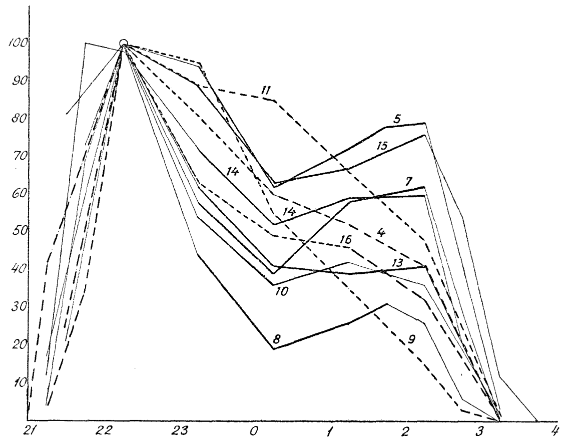

Fig. 3. Activity of the individual nights in the period $^{4}/_{7}$-$^{16}/_{7}$ 1939. —— nigths with a morning maximum — the activity about midnight specially emphasised, ---- nights without any morning maximum. Abscissa: hour, ordinate: number of individuals in percent of the maximum number. The figures on the curves indicate the dates in July. — Pilehuset.

Table I shows the temperature during the whole period of observation in the time before and during the late maximum; the italicised figures indicate the temperatures of the nights in which the late maximum did not occur; it will be seen that when the temperature falls to 12—13 °C.[1]), temperature becomes a master factor and inhibits the accelerating influence

[1]) Registered at a height of 1.5 m.

of the light. The limit of 12 °C. of course only applies to this particular population in July; later in the year, when species with other temperature demands fly, the limit of the activity will be lower.

The late maximum is most frequently the smallest

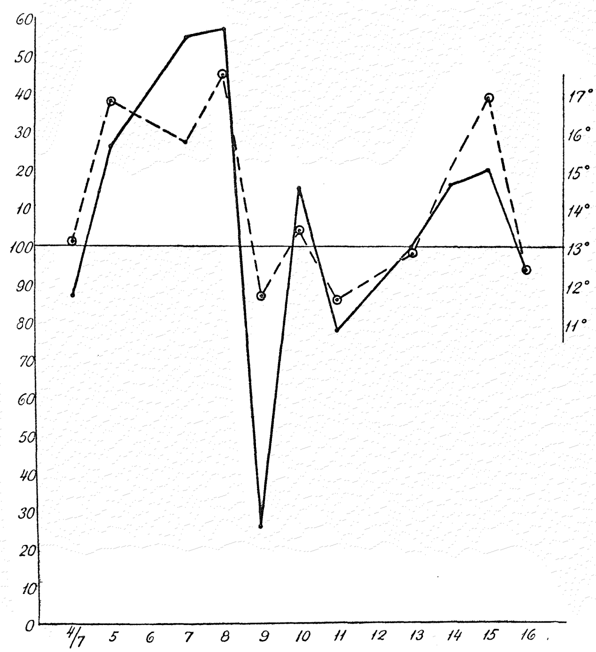

Fig. 4. Comparison between temperature and morning maximum. —— maximum number of individuals after midnight in percent of the stock at midnight. — — The temperature at the time. Abscissa: dates in July 1939; ordinate: the percentages. — Pilehuset.

— and for several reasons; thus some of the individuals have satisfied their hunger during the first part of the evening and accordingly do not fly any more that night, and secondly a couple of the dominant species show a marked preference for flying early in the evening; in the period July 1939 this applied i. a. to *Agrotis pronuba,* which constituted about 50 per cent of the whole population. The variations in the morning stock, however, may be traced to the influence of the temperature. If the greatest number of individuals counted after mid-

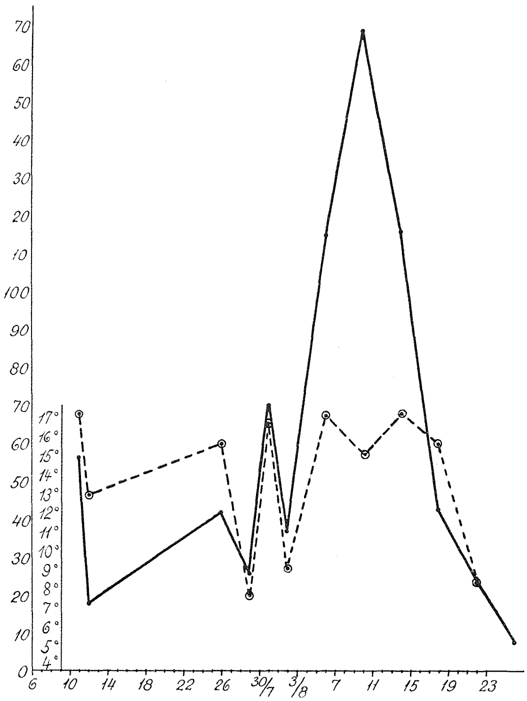

Fig. 5. Comparison between temperature and number of individuals. —— number of individuals per twenty-four hours. — — temperature at 10.15 p. m. Abscissa: dates in July—August 1938, ordinate, left: number of individuals; ordinate, right: temperature. — Pilehuset.

night is plotted against the temperature read at the same time, there will be a distinct correlation between the temperature and the number of individuals, as seen in Fig. 4.

The last-mentioned observations are derived from the observation series made at Pilehuset, where the temperature is most frequently found to be the master factor and the activity consequently seen to follow it. This is because the terrain is damp and sheltered from the wind by birch wood. The humidity of the air and the force of the wind will therefore in most cases range around the optimal values, whereas the locality, owing to its low position, is a cold area with great temperature fluctuations and astonishingly low temperatures in nights

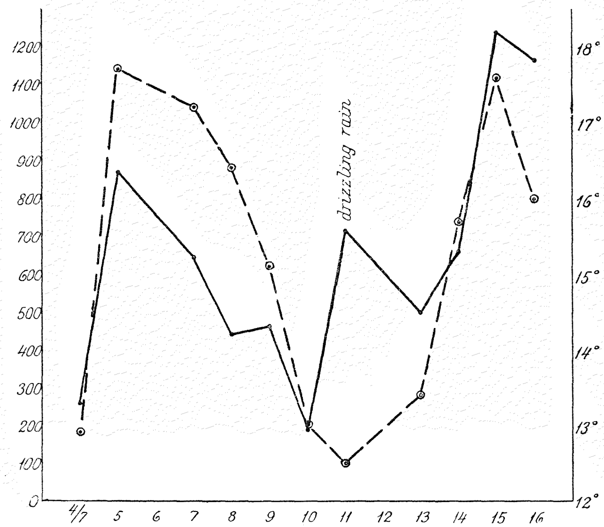

Fig. 6. Comparison between temperature and number of individuals July 1939. —— number of individuals per twenty-four hours. — — temperature at 10.15 p. m. Ordinate, left: number of individuals; ordinate, right: temperature. Abscissa: dates. — Pilehuset.

in which there is radiation. Figs. 5 and 6 show the temperature and the total number of individuals counted per evening during two different periods. The agreement between temperature and intensity of activity is obvious[1]).

The same is shown in Fig. 7, but here the transitional periods mentioned in the introduction make themselves felt. For the case is not so simple that the activity

[1]) As regards Fig. 5, cf. text p. 354.

may be said to increase with increasing temperatures; the individual species of which the population is composed must necessarily be taken into consideration. Each species has an optimal temperature at which its activity is liveliest, and a minimum temperature below which its activity stops. If the temperature rises from the minimal to the optimal, the activity will increase;

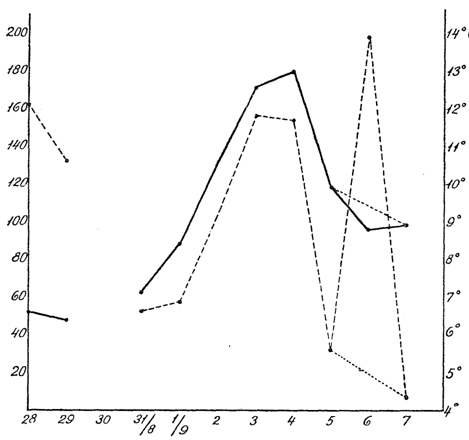

Fig. 7. Comparison between temperature and number of individuals in August—September 1939. —— number of individuals, ----- temperature at coldest place of observation at 8.45 p. m. Ordinate, left: number of individuals, ordinate, right: temperature. Abscissa: dates. — Pilehuset.

if it rises above the optimal temperature, the activity will decrease again. The cause of the increasing activity at rising temperatures, as shown in Figs. 5, 6, and in part in Fig. 7, must therefore be that the temperature has not yet risen above the optimum temperature of the dominant species. The activity curve shown in Fig. 7 follows the temperature fairly well except on September 6th, when an exceptionally warm night caused a small drop of the curve. Table II shows the intensity of the activity of the individual species.

Table II.

	5/9	6/9	7/9
Agrotis pronuba	0	3	1
Amphipyra tragopoginis	1	6	0
Orthosia circellaris	18	9	24
Orthosia lota	2	0	4
Xanthia lutea	8	3	11
Xanthia fulvago	8	6	10
Agrotis c-nigrum	16	10	3
Agrotis xanthographa	8	4	0
Catocala nupta	20	13	13

It will be seen from the table that the warm night caused an increase in the activity of the few pronounced summer species left, for instance *Agrotis pronuba* and *Amphipyra tragopoginis,* but the temperature was above the optimum of the late autumnal species *Orthosia circellaris, Orthosia lota, Xanthia lutea,* and *Xanthia fulvago,* and inhibited their activity. The dominant species of the period, *Agrotis c-nigrum, Agrotis xanthographa,* and *Catocala nupta,* which were rapidly declining to the benefit of the late autumn species, have been inserted for comparison.

The Force of the Wind as a Master Factor.

Under other physical conditions, however, the correlation with the temperature ceases; this is seen i. a. from Fig. 8 from Tipperne, June 1940, when the activity was almost antagonistic to the temperature. An analysis of the individual species will show that this is not due to the optimum temperature having been passed; accordingly other factors must exert their influence. However, there is no accordance with the humidity of the air, but the activity follows the force of the wind.

The last-named observation led to a closer investigation of the influence of the force of the wind and of the evaporation on the activity of the insects in the locality Tipperne. It is a bare and entirely unsheltered meadow locality; the humidity of the air is great, and owing to its situation near the sea the temperature fluctuations are mostly moderate, whereas the force of the wind is often subject to great fluctuations.

In order to find out whether the Noctuids on the whole react to the movements of the wind, two boxes with food were placed on the same post, one on the windward side, the other on the lee side. A series from Tipperne, 1942, is given in Table III; Box A was turned towards the south, Box B towards the north. The Noctuids flew against the wind, attracted by the smell, then they circled for some time around the post before settling down. Table III shows the results of some counts in August.

Table III.

Date	Box A	Box B	Direction of the wind
8/8	0	7	South 1—2
9/8	1	20	Southeast 2
10/8	0	16	Southeast 3
11/8	0	0	Southeast 3, rain
12/8	0	2	Southwest 5
13/8	22	4	Northwest 3

It will appear from the table that the Noctuids react distinctly to the movements of the wind and show a predilection for the leeward box.

On a closer investigation of the influence of the wind on the evaporation it was found, among other things, that the evaporation from a controlled body, placed at the same height as the food boxes, increases proportionally with the force of the wind with about the same saturation deficit[1]) (Fig. 9). Whether this also applies to the Noctuids, is not known; however, when these, as actually appears from Table III, react to the action of the wind, there is a specially good chance of finding pro-

[1]) The term saturation deficit, M, is used instead of relative air humidity, RH, because the temperature is included in the former. $M = E(100 - RH) : 100$. $E =$ the pressure of the saturated vapours at the temperature in question.

portionality, just as regards the intensity of the activity, with the force of the wind measured, if such a proportionality is actually present. The reason for this is as follows: 1) During flight the Noctuids move at a height above the ground at which the wind is strongly active and where the force of the wind may be readily registered; 2) the Noctuids move against the wind to find

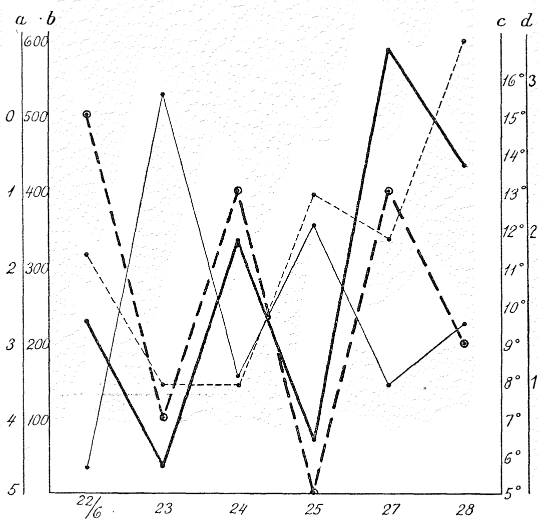

Fig. 8. Comparison between number of individuals —— in June 1940, and temperature ——, force of wind — —, and saturation deficit - - - -. Abscissa: date. Ordinates: a, force of wind, b, number of individuals, c, temperature, and d, saturation deficit. — Tipperne.

the waves of fragrance which are to show them the way to the sugar bate, and thus we may be fairly certain that they are actually exposed to the force of wind registered; 3) during the flight the metabolic processes increase so considerably that the spiracles must be kept open, and consequently the chief way of reducing evaporation is excluded and one of the most frequent complications in investigations on the evaporation of insects avoided.

Throughout the month of July 1942 the present author made observations in Tipperne on the dependence of the activity on the force of the wind. The result is shown in Fig. 10. The force of the wind is given according to Beaufort's scale. The temperature was very stable except during the first few nights, while the force of the wind fluctuated considerably. The activity does not seem to have any relation to the temperature

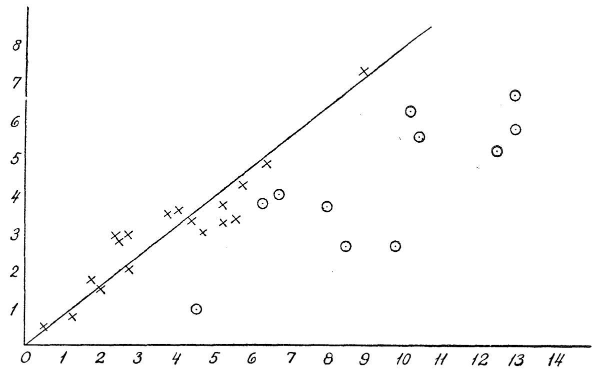

Fig. 9. Relation between force of wind and evaporation, + saturation deficit between 0 and 2, ⊙ saturation deficit above 2. Abscissa: loss of water in mg. Ordinate: force of wind after Beaufort's scale. — Tipperne.

or to the saturation deficit, but there is a distinct correlation between the activity and the force of the wind. The same applies to the period in August (Fig. 11); here, however, the activity was particularly low during the first days of the period because several factors were at the same time near the minimum demand (cf. below).

From the three examples mentioned, from June 1940, July 1942, and August 1942 (Figs. 8, 10, and 11), it will be seen that in unsheltered places the force of the wind often approaches the minimum demand and accordingly dominates over the other factors as the master factor. Since, owing to the radiation, low forces of the wind and calms frequently occur in association with low temperatures, and the reverse, we may often find that while the activity in sheltered localities follows the temperature, it is the antagonist of the temperature in unsheltered places.

The inhibiting influence of the wind is in part mechanical: the increased resistance during the flight and the discomfort caused by the collar being blown up and

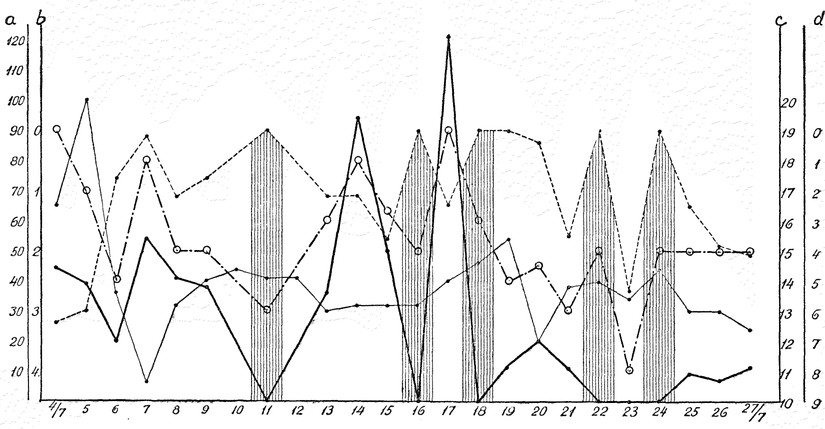

Fig. 10. Comparison between number of individuals —— in July 1942, temperature ——, force of wind —·—, and saturation deficit ----. Vertical ruling from the curve showing the saturation deficit indicates rain. Abscissa: date. Ordinate: a, number of individuals, b, saturation deficit, c, temperature, and d, force of wind. — Tipperne.

the wings fluttering distinctly affect the animals and induce them to seek shelter. Moreover, the increased evaporation due to the movement of the wind plays a considerable part; thus the force of the wind cooperates with the temperature and the humidity of the air, because the evaporation depends on the saturation deficit. In this way further complications may arise, both low and high temperatures in connection with great forces of wind having an inhibiting effect, the former owing to cooling, the latter owing to an increased evaporation. In addition it is, no doubt, of importance that at great forces of wind the waves of smell from the food will be dissipated and thinned, so for that reason alone a smaller number of Noctuids will approach the sugar bate.

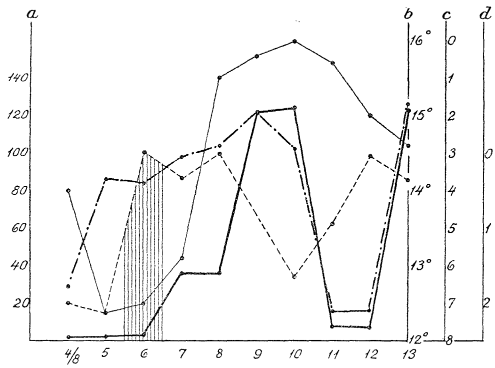

Fig. 11. Comparison between number of individuals —— in August 1942, temperature ——, force of wind —·—, and saturation deficit ----. Abscissa: date. Ordinates: a, number of individuals, b, temperature, c, force of wind, and d, saturation deficit. — Tipperne.

Humidity of the Air and Precipitation as Master Factors.

In this country the relative humidity of the air is rarely so low in the night that it becomes a marked master factor. However, a single example is at hand from Tipperne from June 1939, when the activity ceased almost entirely owing to an abnormally low humidity of the air. On the other hand, a combination of a relatively low humidity of the air and a high temperature may at times result in so high a saturation deficit that the activity is distinctly reduced. Examples of this are supplied by July 4th and 5th, 1942, when comparatively few animals flew in spite of favourable conditions (Fig. 10). These two days showed the absolutely highest saturation deficits during the period, viz. 3.2 and 3.0 respectively. As stated above, the same applies to August 4th and 5th, when the activity was less than expected by the author, even though the conditions could not be characterised as favourable (Fig. 11).

Great humidity of the air is always favourable, and a fine drizzling rain does not, as a rule, give rise to a decrease at first — the contrary is the case (cf. Fig. 6). A regular downpour, however, will always have an inhibiting effect, and the consequence of a shower of rain may persist for many hours. Precipitation may often be seen to act as a master factor and to govern the activity in spite of favourable temperature, light, and wind conditions. On July 11th, 16th, 18th, 22nd, and 24th, 1942, it rained, and the activity ceased entirely even though the other climatic conditions were fairly good (Fig. 10). On August 6th, 8th, 11th, and 12th it likewise rained, and the activity nearly ceased; however, on these days the other conditions were not good either, so it is difficult to conclude anything about the influence of the precipitation (Fig. 11). Thus in Skallingen, Tipperne, and other unsheltered localities precipitation often means a catastrophy, because the activity ceases completely; but in sheltered terrain rain frequently only means a change of phase and a reduction of the activity. Fig. 12 shows examples of the influence of the precipitation in sheltered terrain. On August 19th and 26th it rained in the early evening, but the temperature was especially favourable; the average activity curve for the whole month (August 2nd—September 2nd) has been inserted in the figure for comparison; it will be seen that the avtivity is not only reduced, but it has also been shifted sideways, so that the influence of the light, too, is dominated by that of the precipitation.

It is not easy to say why the precipitation plays such a great role even after it has ceased; a concurrent cause, is no doubt cooling due to the increased evaporation, from the surroundings as well as from the damp Noctuids themselves when they are to fly; for it is characteristic that the animals often fly briskly during the beginning of a shower, but then stop their activity even if the shower ceases. Moreover a too lively activity is always unfortunate in wet surroundings, because the

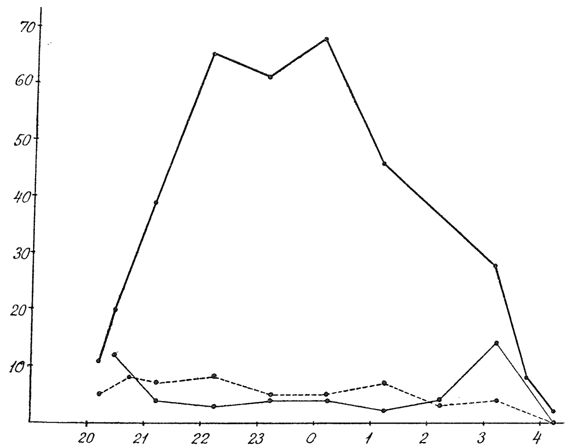

Fig. 12. Influence of precipitation on intensity of activity. — average curve for the period August 1938, — and ---- activity curves for two rainy nights. Abscissa: hour; ordinate: number of individuals counted. — Pilehuset.

wings are liable to adhere to the surroundings, when the scales will be rubbed off. Finally the cause of the slight activity may perhaps be that the odoriferous substances are absorbed by the rain drops, the Noctuids being accordingly attracted by a less intense smell; they will therefore often be seen to keep quiet in rainy weather.

Hunger as a Master Factor.

As stated above, the primary cause of the activity measured is hunger, while the first inhibition of its manifestation is the light, which is the master factor at a certain intensity of light. Hunger makes itself felt every twenty-four hours, and every twenty-four hours include periods of unfavourable intensity of light as well as periods of favourable light intensities. It may happen, however, that a number of the other important factors: temperature, air humidity, force of wind, and precipitation, for several consecutive nights are near the minimum. Concurrent circumstances may cause now one now the other factor to lie below the minimum limit so that during some period there will be no activity at all in the night. One of two things may happen: either the animals will die as a direct consequence of the hard weather, being weakened and more easily falling prey to enemies, or they will die from starvation when they have had no food for several nights. In the experiments with *Agrotis pronuba* (p. 354) it was observed that the activity lasts the longer the more hungry the animal is, and after some days it will look for food throughout the whole dark period, after which it will soon die.

Both on Skallingen and Tipperne the author observed a different result of unfavourable conditions during the normal time of flight, since as regards a number of species hunger will become the master factor and dominate the inhibiting influence of the light, with the result that the Noctuids will fly about seeking food by daytime instead of during the night. In Tipperne such periods often occur in the autumn, and the following observations are derived from that locality. A diurnal activity can, of course, only take place if the weather is better in the daytime and the species are such to which the light is no very great obstacle. These conditions were present for instance in August 1941 and 1942. A period of extremely bad weather was succeeded by a period in which the rain came principally in the night and the temperature was fairly high in the day. The following species were observed to fly by day during the period:

Table IV.

Species 1941	Number	Species 1942	Number
Agrotis xanthographa	166	*Agrotis vestigialis*	1
Agrotis rubi	14	*Agrotis rubi*	3
Agrotis umbrosa	1	*Agrotis tritici*	1
Agrotis cursoria	2		
Charaeas graminis	166	*Charaeas graminis*	111
Hadena literosa	1	*Hadena literosa*	1
Hadena bicoloria	4	*Hadena bicoloria*	47
Hadena bic. var. striata	2	*Hadena bic. var. striata*	2
Hadena ochroleuca	1		
Leucania impura	1		
Hydroecia nictitans	396	*Hydroecia nictitans*	4
Hydroecia micacea	24		
Heliotropa leucostigma	2		
Plusia jota	1	*Plusia gamma*	5

Fig. 13 shows the twenty-four hour curve for the three commonest species in 1941 as well as the curve for the same species in 1939, for comparison. The investigations on the diurnal activity will not be dealt with in more detail here, it need only be stated that the Noctuids which show a maximum in the middle of the day are those which are most resistant to heat in the laboratory experiments and, moreover, such as occasionally fly in the day under normal conditions also. *Agrotis xanthographa* reaches its maximum late in the afternoon and in experiments is less resistant to heat than the other species; as a nocturnal flier it is in action early in the morning or early in the evening, at times when the intensity of the light is fairly high. It is curious, however, that *Hydroecia nictitans,* which has its maximum as a nocturnal flier at midnight, flies in the brightest sunshine. This is probably connected with the high heat demand of that species. It is not only the light intensity which is unfavourable in the day, but the saturation deficit also is, as a rule, too high, thus in the four days on which diurnal flight was liveliest the saturation deficit was 4.87, 3.92, 4.03, and 3.88 respectively or twice that of the night (cf. Figs. 10 and 11). As a consequence the Noctuids are rarely seen to fly; they crawl cautiously up the flowers from the ground and settle down to feed as near the ground as possible.

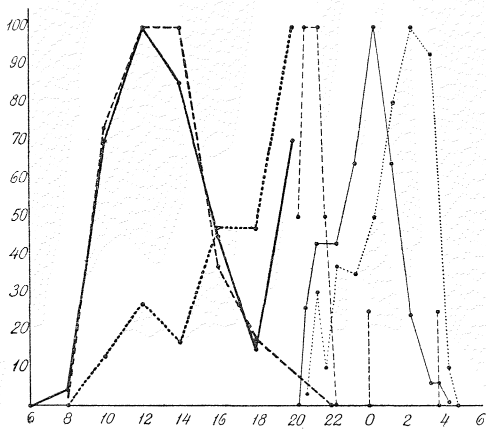

Fig. 13. Twenty-four hour activity of three Noctuids, in 1939 (light curves) and in 1941 (heavy curves). —— *Hydroecia nictitans*, — — *Charaeas graminis*, ... *Agrotis xanthographa*. Abscissa: hour; ordinate: number of individuals in percent of the maximum number. — Tipperne.

Remarks.

Thus the investigation shows that the intensity of activity is governed by the factor that comes nearest to the minimum demands, and since the light passes below the minimum demand every twenty-four hours, it is the factor that sets its mark on the activity as a whole, while the other significant factors, humidity, temperature, and force of wind, are in the main decisive for the degree of intensity. If during a period of some length one or some of these factors lie below the minimum in the night, the hunger of the animals will be so intense that the whole picture of their activity will change phase and the obstacle presented by the light will be overcome.

Dansk Oversigt.

Fra en Undersøgelse over Noctuidernes Aktivitet er her fremdraget en Række Resultater til Belysning af Problemet om Minimumsfaktorers Betydning. Aktivitetsgraden er udtrykt ved det Antal Noctuider, der søger Føde paa udsatte Foderkasser, og der er foretaget Optællinger med bestemte Mellemrum Døgnet rundt i flere Perioder og paa flere Lokaliteter. Samtidig er der foretaget Maalinger af fysiske Faktorer, som Lysstyrke, Vindstyrke, Temperatur, Luftfugtighed og Nedbør. Det er vist, at der meget ofte er en udpræget Korrelation mellem Aktivitetsgraden og de fysiske Faktorer, der paa det paagældende Tidspunkt ligger nærmest ved Minimumskravene og varierer stærkest.

Det, der faar Noctuiderne til at søge Foderkasserne, er Sulten, men Optællinger viser, at de kun søger Foderkasserne paa bestemte Tider af Døgnet (Fig. 1a, b, c), og det vises, at dette ikke skyldes, at Dyrene er underkastet en indre Døgnrytme, men at Lyset er Minimumsfaktor og hæmmer Aktiviteten ved høj Lysstyrke og begunstiger den ved lavere Styrke, medens endnu mindre Lys igen er hæmmende (Fig. 2).

I en Periode svinger Lysets Styrke regelmæssigt Døgnet rundt; naar Aktiviteten ikke svinger ligesaa regelmæssigt, skyldes det, at andre Faktorer optræder som Minimumsfaktorer, og det vises, at i vindbeskyttet Terrain med stor Udstraaling følger Aktivitetskurven Temperaturkurven (Fig. 4, 5, 6, 7), medens Aktiviteten paa ubeskyttet Terrain tydelig er afhængig af Vindstyrken (Fig. 8, 10, 11). Luftfugtigheden optræder kun sjældent som Minimumsfaktor (smlgn. Fig. 10), og medens 100 % relativ Luftfugtighed og Støvregn er gunstig for Aktiviteten, er stærk Nedbør hæmmende ogsaa over andre Faktorers gunstige Indflydelse, saaledes at der bliver Korrelation mellem Nedbør og Aktivitet (Fig. 10, 11, 12). Naar en Række Faktorer gennem længere Tid har ligget omkring Minimumskravene, saaledes at den normale Aktivitet ved den gunstige lave Lysstyrke er hæmmet, kan Sulten optræde som Minimumsfaktor og overveje Lysets Hæmning saaledes at Noctuiderne søger Næring om Dagen (Fig. 13).