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FLIGHT ACTIVITY IN THE BLOWFLY *CALLIPHORA ERYTHROCEPHALA*, IN RELATION TO LIGHT AND RADIANT HEAT, WITH SPECIAL REFERENCE TO ADAPTATION

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1. INTRODUCTION

Many insects depend for survival on wide dispersal by flight. Small insects are carried about passively by air currents (Hardy & Milne, 1937, 1938; Freeman, 1945; Gislén, 1948; Johnson, 1954) and the displacement of even such a large and powerful form as a locust depends largely on the wind direction during flight (Waloff, 1946; Rainey & Waloff, 1948). Spontaneous flight activity is on the whole most obvious in fine sunny weather, but we have little information on the way in which various weather factors might affect it. The subject is difficult to study in the field because most of the factors commonly change together.

Laboratory studies by Davies (1935, 1936) and Broadbent (1949) have concerned the effect of temperature, humidity, wind speed and light intensity on aphids, and Nicholson (1934) has described the effect of temperature on the flight activity of various species of blowflies. There appears to be, however, no detailed account of the way in which light and radiant heat may operate at intensities comparable to those found in sunshine, and little attention has so far been given to the effects of adaptation. The time course of adaptation is of considerable ecological significance, for the conditions to which insects are exposed in sunny weather consists of a continuous series of changes, arising both from changes in the weather and from movements of the insects themselves. The change in activity in response to any particular change of conditions is therefore closely dependent on the rate and extent of adaptation. The experiments described in this paper were carried out to clarify these matters.

The blowfly, *Calliphora erythrocephala* Mg., proved a good subject for these experiments. Observations were made upon a small population of these insects confined in a transparent chamber in a small wind tunnel, and subjected to changes in the experimental factors over a range of conditions comparable to those normally encountered in the field.

2. METHODS

General methods

The blowflies used in this study were bred in muslin cages, and the more active individuals were selected for experiment by taking those which flew actively about the cage and came to rest on the walls nearest the light. They were used at an age of between 2 weeks and 1 or 2 months, according to the season, and males and females were used together in roughly equal numbers. Flight activity was observed by confining the insects in an oblong celluloid chamber with copper or nylon gauze ends (Fig. 1). Internal measurements were $21{\cdot}5 \times 15{\cdot}5 \times 6{\cdot}5$ cm, and when fitted into the small wind tunnel described previously (Digby, 1955), a current of air could be blown through to keep the temperature relatively constant when using radiation strengths sufficient to produce heating. All observations of activity were visual, the insect chamber having behind and below it a piece of white card against which the insects were silhouetted in such a way that their movements could be followed with ease. Insects were commonly used as groups of forty, the total number of flights seen in 45 sec. (or, when very active, in 15 sec.) being recorded once per minute and reduced to flights per specimen per minute. Little difficulty was experienced in counting their flights up to a rate of about 160/min., an average rate of four flights per specimen per minute. Above this rate the occasional coincidence of several flights necessitated a certain amount of estimation, which is, however, unlikely to lead to errors of observation of more than 5% at a rate of 200 flights/min. (5 flights/specimen/min.). Where necessary, groups of twenty insects were used for confirmatory experiments. A given batch of insects was commonly run for up to 5 hr. unless the members showed signs of excessive fatigue by an unduly rapid fall in flight activity and excitability. After each run the insects were returned to the cages for use later on.

All the experiments were carried out at a constant wind speed of 0·5 m./sec. as measured by a hot wire anemometer and Pitot tube close to the centre of the wind channel immediately down-wind from the insect chamber. As the insects were distributed and moved about the chamber more or less at random, those flying through the centre were subjected to wind of the measured velocity, while the others at rest on the sides would experience lower speeds.

The air in the tunnel was usually in free circulation with that of the laboratory, temperature being raised as necessary by heating elements in the tunnel. Most of the experiments were carried out over a period of time, the temperature and humidity, measured by wet- and dry-bulb thermometers, ranging from 17·0 to 25·8° C. and from 45 to 73% R.H. between experiments. In any one experiment at or below light intensities of 2600 lux the temperature was held constant to 1·0° C. and humidity remained steady apart from changes resulting from changes of temperature. Over the range used, variation of temperature and humidity between experiments has negligible influence on the magnitude of the reaction to light, and the results are therefore considered as one group.

Temperature profiles within the insect chamber were measured by a fine copper-constantan thermocouple used with a unipivot galvanometer type LX.

Light and radiant heat

Light in the range from 20 to 41,000 lux was supplied by tungsten gas-filled bulbs mounted vertically overhead. To keep the colour approximately constant, light intensity was adjusted by using one of a series of bulbs of various strengths (2 kW., 150 W. and 15 W.), by moving the particular bulb up or down, and by inserting various thicknesses of wire gauze or paper between it and the insect chamber. The 2 kW. bulb was under-run to reduce its colour temperature to approximately that of the others and to lengthen its life. Intensities below 20 lux were obtained by using a small 3·5 V. bulb with an opal and various neutral filters. The observer wore heavily smoked glasses during the initial periods at high light intensity and removed them when the light was reduced, to ensure a sufficient degree of dark-adaptation to be able to see the insects during the period at low intensity.

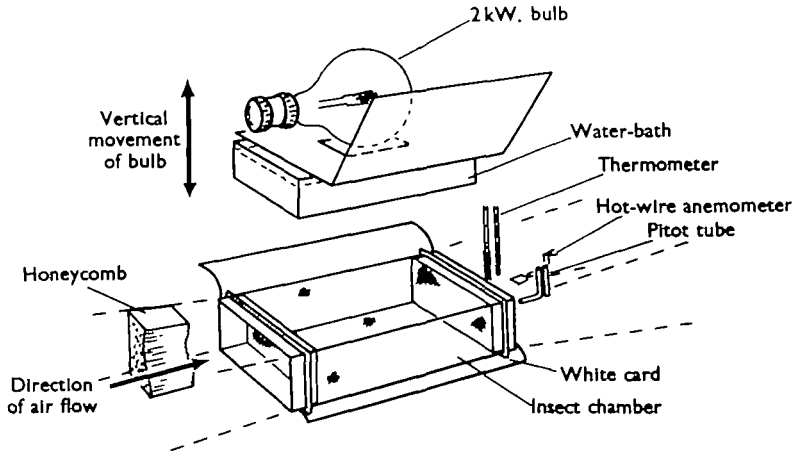

Fig. 1. Diagram showing arrangement of light, water-bath and insect chamber.

Light intensity was measured at the centre of the insect chamber by a Weston photographic exposure meter covered by a diffusing opal or by a selenium photocell with an opal and a Cambridge unipivot galvanometer, the instruments being calibrated against a 1000 W. standard photometric lamp at 2854° K. Radiant heat was measured by a small pyrheliometer (Digby, 1955).

The 2 kW. bulb was used with a 3·5 cm. depth of water in a Perspex trough as a heat filter, increasing the efficiency of the radiation to approximately 34 lumens per watt. This is below that of daylight when there is little or no cloud, which ranges between roughly 80 and 125 lumens per watt (Atkins & Poole, 1936; Blackwell, 1954 and personal communication). Values of illumination at and above 2600 lux in these experiments therefore cause roughly three times as much heating as do the corresponding illumination intensities of daylight. Heating by the other bulbs used

without the water-bath is roughly twice as great for any given light intensity, bu at the strengths used this was unimportant.

Conditions were varied over a range of values of the same order as those found in the field. Illumination ranged up to 87,000 lux, while the maximum for daylight is above 130,000 lux in summer with brightly lit cloud in the sky. Radiation intensity ranged up to 3·2 cal./cm^2./min., while the maximum radiation for daylight is a little above 1·5 cal./cm.^{2}/min. or possibly about 2·0 cal./cm.^{2}/min. when all sources are considered. Air and surface temperatures in the experiments were comparable to those found under the conditions prevailing close to the ground in summer.

3. ACTIVITY IN THE INDIVIDUAL AND IN THE POPULATION

Activity in the individual

In any individual the activity shown in the insect chamber at any one moment may be referred to one of four phases: quiescence, grooming, walking and flight. In one set of experiments individual insects confined in the chamber were watched under constant conditions for periods of 1 hr., while their activities were recorded continuously on a kymograph by a lever which could be moved between four positions corresponding to these main phases of activity. Each insect was acclimatized for 10 to 20 min. before observations began, and conditions were maintained constant at a light intensity of 2600 lux, a wind speed of 0·5 m./sec., and an air temperature at a figure between 22 and 25° C. Two of these records (Fig. 2) show how the activity pattern of an individual can be remarkably uniform, but equally well can exhibit strong periodicity, such as an alternation between periods of 5 or 10 min. during which frequent flights were made and periods of 20 min. of relative rest during which no flights were made at all. Very young and active individuals do not at first show such marked periodicity, but with older insects, as used for most experiments, six out of eleven specimens showed such periodic behaviour. This periodicity in activity renders unpractical the use of single individuals for the study of the relation between activity and stimulus.

Activity in the group

If, however, a sufficiently large group of individuals is studied as a whole, the average activity becomes sufficiently smoothed to permit the average relation of activity to stimulus to be followed with some degree of confidence. Fig. 3 shows how the flight activity of a group of forty flies decreases with reduction of light intensity, the insects showing marked photokinesis; 'high photokinesis' in the terminology of Fraenkel & Gunn (1940).

It is desirable to observe as large a group of insects as possible in order to reduce the irregularities arising from individual behaviour, but owing to the limitations of visual recording a group of forty flies proved most convenient.

Mutual stimulation

In considering such changes in the average activity of a group it is necessary to investigate possible interaction between individuals. In the breeding cages under

quiet, warm conditions and low illumination there is often an alternation in activity of the whole population, periods of very active flight alternating with periods of almost total quiescence. Such obvious periodicity in the behaviour of the group as a whole did not occur in the insect chamber under the conditions described, suggesting mutual stimulation to be less than in the breeding cages.

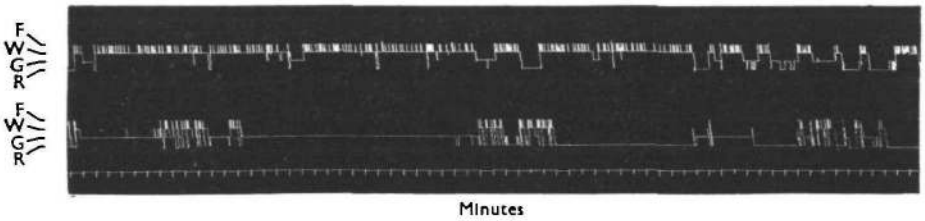

Fig. 2. Activity of two individual specimens of *Calliphora* in the insect chamber, showing continuous and rhythmic activity respectively. F, flights, W, walking; G, grooming; R, at rest. Time marker in minutes.

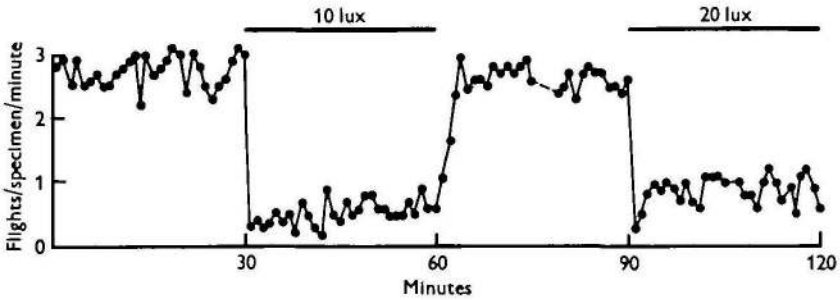

Fig. 3. Activity of a group of forty specimens, in a typical experiment during which the light intensity was changed from 2600 to 10 lux and back, and to 20 lux and back. The curve shows the decrease of activity with decrease of light intensity followed by a certain amount of recovery.

It is reasonable to suppose that such interaction, if it occurs, will be a function of the total rate of activity in the chamber, and will therefore lead to a change in the average rate of flight activity when the number of insects in the chamber is varied, other factors remaining constant.

Two series of experiments were therefore carried out to investigate the effects of crowding. Both were carried out at 2600 lux and at 17·0° or 22·0° C. maintained constant to 0·25° C. by means of a heating element in the air stream.

In the first series the activity of a single marked individual was investigated in relation to the presence of four similar unmarked individuals. In half the experiments one marked and four unmarked flies were confined in the chamber for 20 min. to become acclimatized, and then for a further 40 min. during which the flights were recorded. Half-way through the period of observation the unmarked members were removed quietly by a suction tube allowing comparison of the activity of the marked fly before and after the removal of its fellows. The other half of the experiments was carried out in reverse, the marked fly being acclimatized and observed alone for the first half of the 40 min. period of observation. Recently emerged insects

were used in order to reduce periodicity to a minimum. In a series of fourteen experiments the mean activity of the marked fly (average 1·57 flights/min.) showed a significant increase of activity by $57 \pm 26\%$, standard error ($P < 0{\cdot}05$), in response to the presence of the other four.

In the second series of experiments, the average activity of groups of five, ten and forty flies were investigated in relation to the number in the group. Each group was acclimatized for 20 min. and then observed for a further 20 min., the average activity being compared with that of a control group of twenty treated in a precisely similar manner and run immediately beforehand. Precautions were taken to make sure that the experimental and control groups represented similar random samples of the same stock. The results are shown in Table 1. The average activity showed no significant increase with crowding between groups of five and groups of forty, activity with ten in the chamber being even slightly greater than with the larger control group.

Table 1. *Effect of crowding on activity with between 5 and 40 flies in the chamber*

No. in experimental group ...	5	10	40
No. of experiments	11	5	5
Mean activity of control group of 20 flies (flights/specimen/min.)	7·32	5·91	5·00
Difference in activity of experimental and control groups, as percentage of activity of control group (with standard error)	$+11\% \pm 12\%$	$+14\% \pm 3\%$	$+2\% \pm 3\%$

Thus, although crowding probably leads to some increase of activity at low density, at higher densities there is little or no effect. As mutual stimulation might be expected to be more effective at higher densities, this suggests that two antagonistic factors may be operating, but investigation of this matter must await further study.

These insects were very active, flights being made at the rate of about 200/min. with forty flies in the chamber, and the experiments with varied numbers of insects cover the range of total activity normally observed in the group of forty. If our original supposition is correct—that is, if mutual stimulation occurred it would result in change of activity with crowding—we may conclude that these effects are small enough not seriously to invalidate the results of experiments on the reactions of a group to sensory stimuli. The conclusions reached in this paper are subject to such mutual stimulation as does occur.

4. ADAPTATION AND THE RESPONSE TO LIGHT

Adaptation

Changes of activity resulting from changes of light are subject to adaptation. Thus the decrease of activity of a group of forty flies resulting from a decrease of light intensity (Fig. 3) was followed by a certain amount of recovery; a family of

curves showing such recovery is given in Fig. 6. This goes on for a long time, as is shown by Fig. 4. Curve *A* illustrates the activity during ½ hr. at 2600 lux followed by about 4 hr. at 5·2 lux, and finally by ½ hr. at 2600 lux again. The low level of activity reached shortly after the decrease of light showed a slow increase of about 50% in 5 hr., and when the light was returned to 2600 lux, activity became greater than at the beginning of the run. When the changes were made in the reverse order (curve *B*), activity during the long period at high light intensity showed a slow decrease.

This return of the rate of flight activity towards that existing before the change is an adaptation of population activity, and the term adaptation is used here in this sense, without prejudice as to the nature of the adaptation. Whether it arises as nervous adaptation or through some other factor not connected with the nervous system is not within the scope of this paper.

Because of these adaptive trends the change of activity following a change of stimulus must be related to a particular time interval after the change.

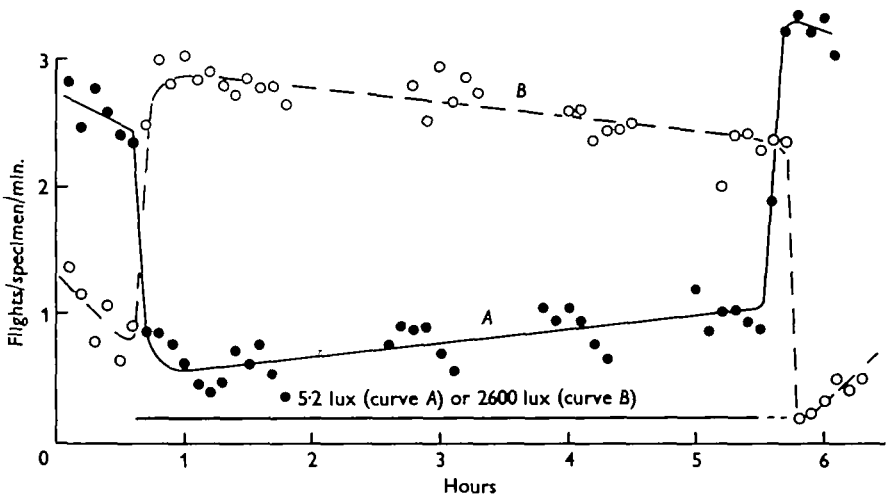

Fig. 4. Activity of a population over a period of 6½ hr. during which the light intensity was changed from 2600 to 5·2 lux and back (curve *A*) and from 5·2 to 2600 lux and back (curve *B*) showing long-term adaptive trends in each case.

The relation of activity to light intensity

Analysis of the relation between change of activity and change of light intensity in a group of insects demands that the initial state of the insects with regard to light-adaptation shall be constant. The time required for complete adaptation is so long that it is out of the question to adapt the insects fully to the initial light intensity before each change. It was found practicable to subject a group of forty flies to a convenient standard intensity of 2600 lux for ½ hr. at the beginning of each experiment and to regard them as relatively adapted to that intensity during the last 10 min. This initial period was followed by ½ hr. at an experimental light intensity,

after which the light was returned to the standard for a further ½ hr. as the beginning of the next experiment. Two such experiments are shown in Fig. 3; a number of them were commonly carried out in a day, during which the activity at the standard value would usually show a decline. This decline, an adaptation remainder so far as these short-period experiments are concerned, arises partly from the fact that the initial light intensity of 2600 lux was stronger than that maintained in the cages and in the insect chamber prior to the experiments.

To make the various experiments comparable, activity at each experimental intensity was expressed as a percentage of that during the last 10 min. of the preceding standard period. This method is not without its drawbacks, for the percentage change of activity at a given light intensity does vary with large changes in the excitability of the stock, as is shown by Fig. 4. This treatment was, however, adopted for convenience, for among the possible simple methods of comparison it gave the greatest consistency in repeated identical experiments.

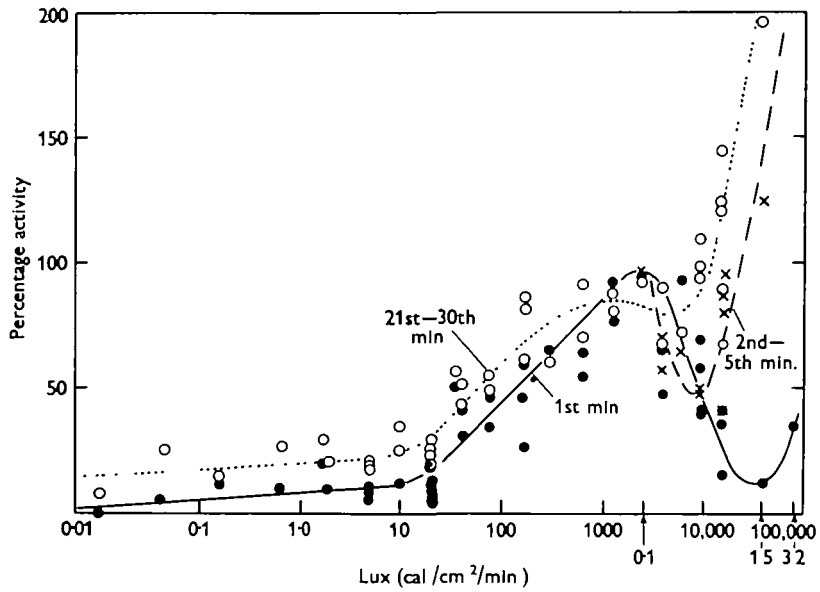

Fig. 5. Activity following a change in light intensity at various periods after the change. Activity expressed as a percentage of that prevailing during the last 10 min. of the preceding period at 2600 lux.

Curves relating the change of activity to change of light intensity are given in Fig. 5 for the periods of the first, the second to the fifth and the twenty-first to the thirtieth minutes after the change. These experiments were carried out over a range of temperatures (18·4–25·8° C.) and humidities (45–73 % R.H.). Details are given in Table 2. Correlation coefficients (Fisher, 1925–50) relating the magnitude of the change of activity to these factors showed them not to be significant ($r = 0{\cdot}08$, $n = 44$, $P > 0{\cdot}05$ and $r = 0{\cdot}003$, $n = 23$, $P > 0{\cdot}05$, respectively).

Table 2. *Relation between change of activity and change of light from 2600 lux to experimental value, with temperature and humidity at which experiments were carried out*

Experimental value of light (lux)	Temperature (° C.)	Humidity (% R.H.)	Activity 21–30 min. after change (%, see text)	Experimental value of light (lux)	Temperature (° C.)	Humidity (% R.H.)	Activity 21–30 min. after change (%, see text)
	In last 10 min. of initial period at 2600 lux				In last 10 min. of initial period at 2600 lux		
0·0002	20·6	—	0·083	1·6	24·0	—	0·55
0·0008	21·6	—	0·26	3·2	19·2	68	0·61
0·0032	21·6	—	0·17	3·2	25·8	—	0·82
0·013	21·6	—	0·28	3·2	25·0	—	0·87
0·035	19·7	68	0·30	6·5	21·3	56	0·60
0·05	23·9	—	0·21	13	20·2	66	0·71
0·1	18·4	65	0·22	13	23·0	—	0·92
0·1	18·5	65	0·18	25	20·6	65	0·81
0·1	20·6	53	0·19	25	22·0	—	0·89
0·1	23·5	—	0·18	50	18·9	69	0·93
0·2	19·2	64	0·35	79	18·4	54	0·90
0·2	23·7	—	0·26	79	18·7	67	0·68
0·4	18·6	65	0·30	125	21·3	46	0·73
0·4	23·7	—	0·24	190	20·4	52	1·00
0·4	25·0	—	0·27	190	22·6	71	1·10
0·4	24·7	—	0·24	190	20·1	63	0·94
0·4	25·1	—	0·20	310	22·8	45	1·44
0·4	24·8	—	0·24	310	21·8	73	1·21
0·7	21·0	64	0·58	310	22·5	—	0·89
0·8	24·3	—	0·52	310	23·0	—	1·24
0·8	23·8	—	0·44	800	20·6	64	2·05
1·6	18·6	65	0·49	1600	21·5	61	2·92

A small amount of flight activity could be heard to occur in complete darkness, although counts could not be made. At intensities between 0·01 and 10 lux flight activity bears little relation to light. Between 10 and 2600 lux activity increases with light; the heating effects of radiation may be shown to be unimportant at this level and changes of activity are due to light alone. The extent of adaptation over this range, shown by the difference in position of the curves for the first and for the twenty-first to thirtieth minutes, is relatively small compared with the variation in activity with light intensity. Above 2600 lux, which corresponds in these experiments to a radiation intensity of 0·1 cal./cm.^{2}/min., activity shows an initial decrease followed by an increase to values greater than those to be expected from extrapolation of the part of the curve below 2600 lux. It will later be shown that these effects are due to heating.

If we regard light as one of a number of activating stimuli (Wolsky, 1933), the fact that flight activity is relatively independent of light at low intensities suggests that under these conditions other activating stimuli predominate. One of these is certainly wind, for when the insects are left in the chamber in darkness and in still air they become almost completely inactive.

5. MEASUREMENT OF ADAPTATION TO LIGHT

Principles in analysis of adaptation

It was found that while activity decreased rapidly on decreasing the light intensity, the increase of activity which followed an increase of light intensity was a much slower process.

The course of adaptation to greater and to lesser light intensities was studied in order to investigate these differences more fully. The principles employed in this analysis are as follows. The population is subjected to a given level of stimulus until the rate of activity evoked has become steady, when the population may be said to have become adapted to it. If the stimulus is then changed, the extent to which adaptation occurs to the second level can be assessed at any instant by returning the stimulus to the initial level. The curve of activity during the second period at the initial level of stimulus, when the insects are recovering from the effects of the changes, may be called a recovery curve. The difference in activity at the initial level of stimulus, as measured before and again immediately after the period at the second level, is a measure of the amount of adaptation which has taken place to the second level of stimulus. The time course of adaptation may be plotted by carrying out a series of experiments with different values for either the magnitude or duration of the second level of stimulus. Duration has been varied in these experiments.

Adaptation to high light intensity

To analyse the course of adaptation to high light intensity (Fig. 6) the insects were adapted first of all to a low intensity (20 lux) until the activity became relatively constant. They were then subjected to varying periods at a higher intensity (2600 lux), after which the low intensity was applied once more. The second period of low intensity is a test stimulus and the family of recovery curves of activity during this period show the following features: a short period of high light intensity results in an initial depression, a rebound, small in both magnitude and duration, during this second period of low intensity, while a longer period of high intensity results in a greater and a longer depression. The activity at any particular moment during this test period differs from that at the end of the initial period at low intensity by an amount which is a measure of the adaptation to the higher light intensity at that moment. This adaptation to the experimental value is maximal at the first instant of the test period, after which there is re-adaptation back to the initial level. The initial values of a family of these recovery curves form an adaptation curve (Fig. 6, broken line), relating the extent of adaptation to the duration of the adapting stimulus. This adaptation curve is somewhat diagrammatic, as it is compounded from experiments carried out on different occasions with stock not always of identical age and sensitivity. Nevertheless, it can be seen that the most rapid part of adaptation to high light intensity is complete in 20 min. or $\frac{1}{2}$ hr.

Adaptation to low light intensity

Adaptation to low light intensity was investigated by using the same intensities in the reverse order. The effect of periods of low light of varying duration was studied by observing the activity during the following periods of high light. This family of curves (Fig. 7) is not a mirror image of the family of curves in Fig. 6; there is no obvious rebound. Indeed, the two sets appear at first sight to be remarkably

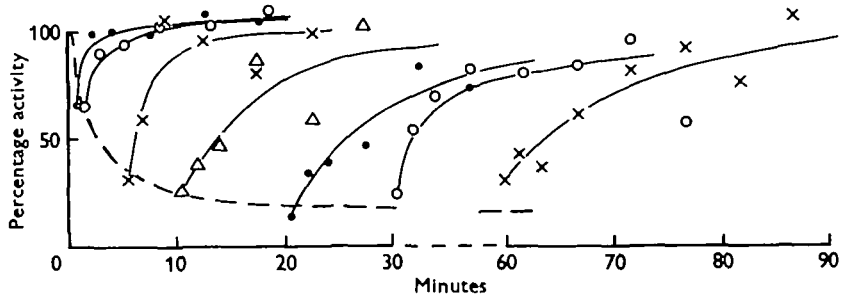

Fig. 6. Adaptation to high light intensity (i.e. family of recovery curves at 20 lux after varied periods at 2600 lux during which the activity was much greater). The broken line, passing through the initial point of each curve, shows the time course of adaptation to 2600 lux. Activity expressed as a percentage of that prevailing during the last 10 min. of the initial period at 20 lux, time as minutes elapsed since the end of this initial period.

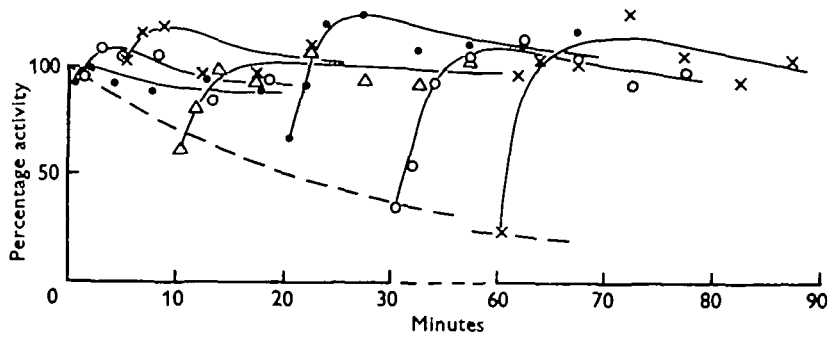

Fig. 7. Adaptation to low light intensity (i.e. family of recovery curves at 2600 lux after varied periods at 20 lux during which the activity was much less). Activity expressed as a percentage of that prevailing during the last 10 min. of the initial period at 2600 lux, time as minutes elapsed since the end of this initial period.

similar. After a period at low light intensity the activity of the insects in the first few minutes shows only a slow rise to a level a little higher than that prevailing initially.

This persistence of a state of low activity is not the result of complete lack of activity or akinesis in a certain proportion of the members, for they are all more torpid. It was necessary to ascertain whether this state of low activity might be due entirely to change in light intensity, or whether heat might be an important additional factor. Heating causes an initial depression of activity, and although but

little heating is involved at 2600 lux it seemed desirable to investigate the matter. Experiments on the increase of activity with increase of light from 10 lux to values between 40 and 6400 lux all showed the same slow increase of activity with increase of light, however, and as heating effects were very small indeed at these lower light intensities, we may conclude that the state of persistent low activity arises entirely from changes of light intensity.

Peaks of activity can be traced in the recovery curves at times varying from 3 to 15 min. after the resumption of high light intensity. After this peak in each recovery curve, the trend becomes the mirror image of that of the recovery curves following a period of high light intensity. The initial parts of the recovery curves show that during the preceding low level of stimulation, when activity has been low but rising, the state of persistent low activity had been setting in progressively.

Although the persistence of the state of activity existing before the change is most noticeable in the recovery from a low light intensity, there is also a short lag following the reverse change. Activity commonly declines over a period of from 10 sec. to 2½ min. when light intensity is reduced.

6. THE EFFECT OF STRONG RADIATION

The nature and cause of the reactions to strong radiation

When the light intensity was changed from the standard 2600 to 4100 lux, and above (Fig. 8), there was an initial drop in flight activity for 1–4 min. followed by an increase, usually to a level above that expected from extrapolation of the curve relating activity to light at lower intensities (Fig. 5). There are always, at any one time, a number of insects remaining still or carrying out grooming movements, and during the initial fall in activity this proportion increases so that for some few seconds almost the whole population exhibits these phases of activity. The fact that inhibition of activity is followed by a rise to a final level of activity well above that prevailing before the increase of light shows that at least two reactions must be concerned. We may call the first an inhibition, beginning immediately after the change, and the second an activation, setting in a little later. These reactions may be seen from Fig. 5 to become apparent first above 2600 lux, although the variability of activity in each individual run precludes their detection in any single experiment below about 4100 lux. The minimum intensity of 2600 lux, equivalent to 0·1 cal./cm.^{2}/min., was sufficient to heat the insects by about 1° C., which suggests that the inhibition and activation might well result from the rise in temperature.

If, however, the reactions were due to the perception of illumination the threshold would probably be decreased by dark-adaptation. Thirty-eight experiments had been concerned with the effects of an increase of light to various intensities up to 2600 lux with insects dark-adapted to varying degrees. The increase of activity with increase of light was always delayed by the persistence of a state of low activity, but an actual reduction of activity during the first minute or two only occurred when the intensity was raised to 4100 lux or above, whatever the initial

value had been. This strongly suggests that the effects are not due to light intensity perceived as illumination.

Experiments were therefore carried out to separate the effects of light and heat. Precautions were necessary, for the inhibition is very susceptible to adaptation. In young insects some nine runs on various occasions have shown that the identical reactions can be evoked time and time again, but in older stock (Fig. 8) the general level of activity declines very rapidly and three or four 10 min. periods at a higher radiation strength results in the stock no longer showing inhibition, although activation may still occur. The transitory inhibition may also be lost if the insects have become adapted to heat by crawling close to an exposed electric light bulb in a breeding cage during cold weather. Accordingly, each experiment took the form of a particular experimental change, followed shortly afterwards by the change from 2600 to 16,000 lux as a control, to make sure that the stock was still capable of exhibiting both reactions. Excessive heating effects were avoided.

In one series of experiments strong light intensities were applied while the heating effect was increased by removing the water-bath from beneath the bulb at intervals. When carried out at 6400 lux, inhibition and activation occurred. The average activity change of three experiments carried out in the course of one run is shown in Fig. 9. Two further runs of three successive experiments each gave very similar results. Removal of the water-bath at this intensity caused an increase of the heating effect from 0·25 to 0·47 cal./cm.^{2}/min. for an increase of light of about 15%. As this change in light intensity has in itself a negligible influence in the absence of substantial changes in heat, the effect must be due to heat alone.

To confirm this, a range of intensities of infra-red radiation from an electric radiator fitted with screens was allowed to fall on the chamber at intervals, light intensity being kept at 2600 lux throughout. Three runs comprising ten experiments with infra-red ranging between 0·25 and 0·5 cal./cm.^{2}/min. produced transitory inhibition, sometimes followed by activation depending upon the stock used. The effect of the addition of 0·5 cal./cm.^{2}/min. of infra-red compared with that of an increase of illumination to 16,000 lux (equivalent to 0·63 cal./cm.^{2}/min.) is shown in Fig. 10. As the illumination provided by the radiator represented only a negligible fraction of that provided at the same time by the bulb behind the water-bath, we may conclude that the inhibition must again have been due solely to the heating effect of the radiation.

The reaction to various ways of heating

The heating effect of the radiation in these experiments may operate in various ways. The celluloid surfaces of the insect chamber become heated by absorption of radiation of longer wave-lengths and will warm particularly the tarsi and legs; the warmed celluloid surfaces raise the temperature of the layers of air immediately adjacent to them, which will warm each insect as a whole; and direct absorption of radiation by the insects themselves will cause an increase of temperature in the main body of the insects more than in the appendages. The insects may or may not react to radiation heating in the same way as to an increase of air temperature. As

the organs for the perception of heat may well be localized, it is of interest to know whether there is any difference in the response according to the way in which the heating is applied.

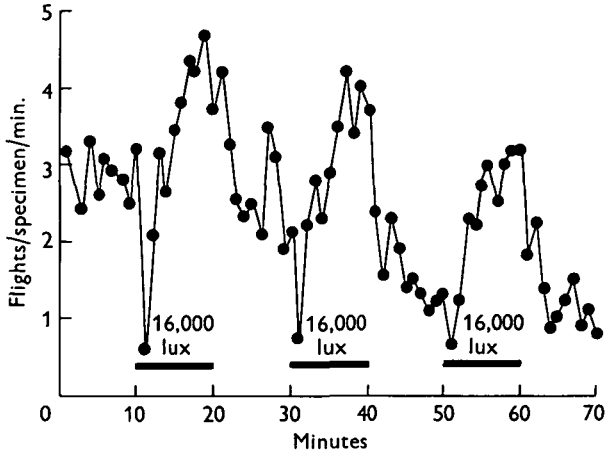

Fig. 8

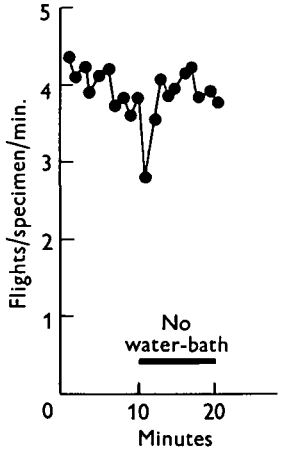

Fig. 9

Fig. 8. Effect of the change from 2600 to 16,000 lux, showing inhibition and activation, and the decline in response with repeated stimuli.

Fig. 9. Effect of removing water-bath from beneath bulb, at illumination strength of 6400 lux. Average of three experiments.

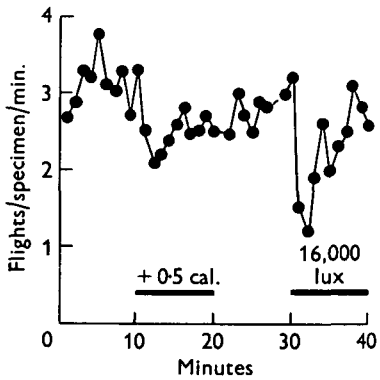

Fig. 10

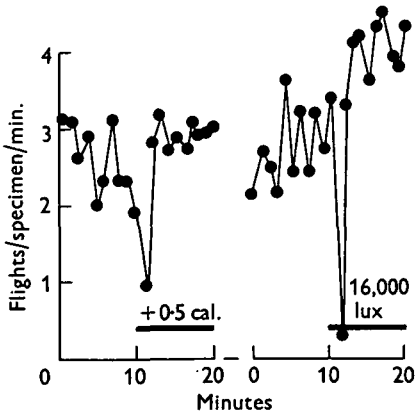

Fig. 11

Fig. 10. Effect of addition of 0·5 cal./cm.^{2}/min. of infra-red radiation from electric radiator to a light intensity of 2600 lux compared with effects of change from 2600 to 16,000 lux, in the usual celluloid chamber.

Fig. 11. Effect of addition of 0·5 cal./cm.^{2}/min. of infra-red radiation to light intensity of 2600 lux, compared with the effect of change from 2600 to 16,000 lux in chamber of nylon mesh.

Measurements of temperature profiles in the insect chamber showed the control change from 2600 to 16,000 lux to be associated with a maximum increase of temperature of 1·75, 1·6 and 0·6° C. close against the surface of the chamber and at distances of 2 and 5 mm., respectively. These distances correspond roughly to the

heights of the upper and lower surfaces of a fly. The temperature excess attained by the thorax of the insect by virtue of its own absorptivity lay between 3 and 7° C. (Digby, 1955).

The effect of a heated surface was eliminated by using a new insect chamber, similar in size but with the celluloid replaced by a fine nylon mesh, transmitting all but about 7% of the light and heat. When fitted in place of the celluloid chamber with the shutters adjusted to obtain a slight positive air pressure, most of the air passed straight through the chamber from end to end, while a part escaped through the meshes, causing the heating of the surface to be quite negligible. In this chamber inhibition and activation occurred as before when a range of values of infra-red radiation was applied at a constant light intensity of 2600 lux (Table 3). Fig. 11 shows the effect of the addition of 0·5 cal./cm.^{2}/min. of infra-red. The effects of radiant heat can therefore be produced when the insects are on an unheated surface.

Heating of the surface itself was investigated with a third type of insect chamber, again similar but with the upper and lower surfaces and the back formed by electrical resistance mats heavily insulated by shellac and with the ends and near side made of nylon mesh. The right-hand end was completely blocked, the air flowing into the left-hand end at 0·5 m./sec. and passing out through the spaces between the wires and through the nylon mesh in front, allowing the surfaces to be heated by an electric current with relatively slight heating of the air inside the chamber. Radiative heating was slight. Again, an appropriate amount of heating gave results very similar to those obtained in the control celluloid chamber (Table 3). Effects similar to those obtained with the controls in the celluloid chamber with a maximum surface temperature increase of 1·75° C. were, however, only produced in the resistance mat chamber with a surface temperature increase of 12° C. Measurement of the temperature profile in this latter case showed air temperatures at 2 and 5 mm. above the surface to have increased by 3·0 and 6·5° C., respectively, which is comparable to the temperature excess developed by the insects in the control chamber. This suggests that perception of heat may depend on temperature changes in the main body of the insect rather than in the legs or tarsi.

The effects of air temperature were studied by fitting a heating element across the wind channel, sufficiently far from the insect chamber for the amount of heat received by radiation to be very slight. The effect of an increase of air temperature is to warm the main body of the insect and the appendages by a similar amount. A fine thermocouple showed that the temperatures across the channel were relatively uniform and reached to within 1·0° C. of equilibrium in less than a minute. Experiments were carried out at 2600 lux, flies being adapted to this light intensity and to a temperature of 20° C. for ½ hr. or more before each experiment. Heating of the air to the appropriate amount caused inhibition and activation in a way similar to that in the control celluloid chamber (Fig. 12, Table 3). This occurred with an increase of air temperature of 5–10° C., of the same order as the temperature excess developed by insects at 16,000 lux in the controls. This suggests that these reactions are due primarily to an increase of temperature of the insects, rather than to the perception of radiant heat as such.

Table 3. *Effect on activity of heating the population in various ways*

Method of heating	Amount of heating	Total no. of experiments	No. showing no effects	No. showing inhibition followed by activation not exceeding initial level	No. showing inhibition followed by activation to above initial level
Nylon mesh chamber (cool surface). Increase of infra-red radiation by	0·3 cal./cm.²/min.	9	9	—	—
	0·5 cal./cm.²/min.	12	7	5	—
	1·0 cal./cm.²/min.	3	—	—	3
Resistance mat chamber (warm surface). Increase of surface temperature by	2° C.	3	3	—	—
	Up to 12° C.	6	1	5	—
	Above 12° C.	6	—	—	6
Celluloid chamber. Increase of air temperature by	5° C.	6	1	5	—
	10° C.	6	1	6	—
	15° C.	4	—	—	4

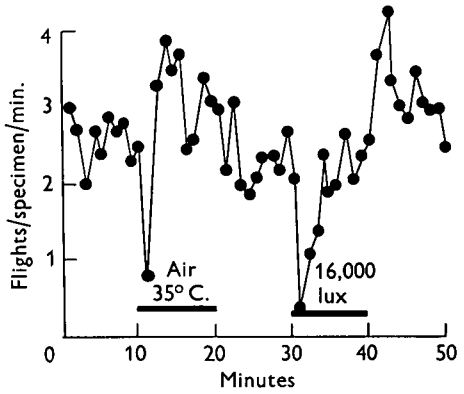

Fig. 12. Effect of an increase of air temperature from 20 to 35° C. and of an increase of light intensity from 2600 to 16,000 lux, in a population of young insects.

7. DISCUSSION

The study of adaptation has been very largely neglected in the field of the relations between insect activity and environmental factors. Adaptation is, however, commonly observed. Thus the curves of activity in alternating light and darkness given by Bentley, Gunn & Ewer (1941) for the beetle *Ptinus tectus* show adaptive trends similar to those demonstrated for *Calliphora*, but with a much longer time scale. In their experiments activity would appear to take an hour or two to reach the extreme value following each change, and the adaptive trend which follows is clearly only partly complete after a further 10 hr. These trends perhaps correspond to the long-term changes illustrated in Fig. 4 of this paper. Broadbent (1949), working with the aphids *Myzus persicae* and *Brevicoryne brassicae*, found that after turning on the light, following a period of darkness during which the insects had become quiescent, activity increased slowly. Activity at a standard low light intensity was low when the light had been reduced from a higher value, but was high, and was

followed by a decrease, when light had been increased from a lower value. These results suggest similarity of behaviour with *Calliphora*. Adaptation also occurs in the relation of activity to temperature, quite apart from the transitory inhibition caused by rapid heating as described in this paper. The differences between the curves of activity of *Lucilia* (Nicholson, 1934) and *Ptinus* (Gunn & Hopf, 1942) at constant and at rising or falling temperatures are a result of adaptive trends, for in this type of experiment the two groups differ in that they have been adapted either to the temperature of observation, or to lower or higher temperatures, respectively. The faster the temperature is raised or lowered, the greater is the difference between that to which the insect is adapted and that to which it is exposed. Such procedure, however, gives very little information on the rate of adaptation to the change of stimulus.

Such adaptive trends are of significance in the ecology of an insect, in that the influence of a particular environmental factor on activity is incompletely defined unless account is taken of the rate of change of the factor as well as its absolute value.

It was shown that a state of low activity induced by a low light intensity tended to persist into a subsequent period of higher light intensity. This persistent state of low activity would appear to have a resemblance to reflex immobilization or akinesis. Reflex immobilization is brought about by powerful inhibitory stimuli, but the effects described here are induced by reduction in the activating stimulus of light intensity. As, however, it is reasonable to suppose that in each individual *Calliphora* a certain background of nervous inhibition is always present, partly at least provided by the stimulus of contact between the legs and the substratum (Fraenkel, 1932; Hollick, 1940), reduction of the activating stimulus of light will, in each insect, alter the balance between activating and inhibiting stimuli in favour of the latter, so that inhibiting stimuli are relatively more powerful at lower light intensities. The state of persistent low activity in *Calliphora* would, therefore, be essentially similar in origin to reflex immobilization, from which it may be considered to differ only in degree.

It is to be stressed that adaptation in this paper refers to adaptation of population activity, and not to that of the sensory end-organs responsible for receiving the operative stimulus.

The transitory inhibition caused by the sharp increase of heat of the appropriate amount was not encountered by Nicholson (1934) or by Gunn & Hopf (1942) in their experiments with blowflies and with *Ptinus*; they would hardly be expected as the rates of temperature increase employed ranged between 3 and 14° C. per hour. The reactions appear in *Calliphora* at rates of 5° C. per minute and upwards. Such sharp temperature changes will often be encountered in the field, and this transitory inhibition produced by heating may well be one factor concerned in the way in which *Calliphora* and other insects bask in the sunshine. Other factors are doubtless also involved, for instance a decrease of activity is caused by increase of temperature above an optimum. Basking involves both orientation and reduction of activity. The former has received considerable attention; thus the orientation assumed by the locust is determined by the internal temperature (Volkonsky, 1939) and it is

adjusted as a result of responses from organs receptive to radiant heat (Slifer, 1951). The transitory reduction in activity in *Calliphora* is not obviously associated with orientation and is evoked by an increase of air temperature as well as by radiant heat, the radiation intensity required in the latter case being such as to suggest that the gross change of temperature of the insect is the causative factor.

8. SUMMARY

1. The spontaneous flight activity of a population of the blowfly *Calliphora erythrocephala* has been studied in relation to light and radiant heat in a small wind tunnel.

2. Flight activity occurs at a low level in the dark under these conditions, and is practically independent of light up to 10 lux. Activity increases sharply with light between 10 and 2600 lux, before heating effects become important.

3. Population activity shows adaptation to light intensity, and a method of analysis is described. The rate of increase of activity following an increase of light is much slower than is the reverse change; the state of low activity at low light intensities tends to persist. Complete adaptation would take at least a number of hours.

4. Heating, which accompanies strong light intensities, causes initially a momentary decrease in activity, usually followed by an increase. Similar reactions occur when the heat is applied in several different ways.

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