

FLIGHT ACTIVITY IN THE BLOWFLY, *CALLIPHORA*
ERYTHROCEPHALA, IN RELATION TO WIND SPEED,
WITH SPECIAL REFERENCE TO ADAPTATION

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INTRODUCTION

Wind speed is prominent among the various weather factors which affect an insect about to take to flight.

Field studies have suggested that wind inhibits the flight activity of, for instance, the desert locust (Waloff & Rainey, 1951), the red locust (Rainey, Waloff & Burnett, 1957), and the tsetse fly (Swynnerton, 1936). On the other hand Vanderplank (1948) found no correlation, and Johnson (1954) a variable one, between wind speed and the catches of the tsetse fly and of aphids respectively. Observations on the activity of locusts early in the morning (Strelnikov, 1936; Kennedy, 1939; Waloff & Rainey, 1951) have suggested that wind may sometimes have an activating effect. The effect of wind in the field is clearly complex and is difficult to interpret as it is usually associated with changes of other factors, in particular of temperature.

Laboratory experiments have shown that wind inhibits flight. Thus Davies (1936) showed this effect in the aphid *Myzus persicae*, and Haine (1955*a, b*) has confirmed these observations and extended them to a number of other aphids. The experiments by Davies (1936) did not show adaptation to wind during the 10 min. periods of exposure to the high wind speed, but experiments by the author indicated that adaptation occurred in the reactions of the blowfly *Calliphora* to wind.

The occurrence of adaptation is important, for wind under the conditions in which insects usually take to flight is normally turbulent, and the effect of wind on activity will therefore depend largely on the rapidity of the reaction to a change of wind and on the extent and rate of any subsequent adaptation.

A study of the flight activity of the blowfly *C. erythrocephala* Mg. in relation to light and radiant heat showed that while individual activity is variable the average activity of a group is relatively uniform and may be related to stimulus with some degree of confidence (Digby, 1958). Further wind-tunnel experiments were therefore carried out in an attempt to clarify the nature of the reaction to wind and the part played by adaptation.

METHODS

General methods

All observations were carried out on groups of flies confined in a celluloid chamber in a small wind tunnel, by procedures similar to those described previously (Digby, 1958). Groups of forty flies between 2 and 6 weeks of age were used for most

experiments. The use of younger flies was avoided because their activity in the chamber often consisted of periods of continued flight and was therefore difficult to assess, and the use of older flies was avoided because their activity tended to fall to a low level and to become very irregular. Unless otherwise stated, the relatively low light intensity of 160 lux was used in order to avoid the possibility of temperature changes due to radiation interfering with results at low wind speeds. The mechanical vibration produced by the fan was found to reduce activity, the flies becoming rather sensitive to it after a period under still conditions. Wind velocity was therefore altered by adjusting the various shutters (shown in fig. 1 of Digby, 1955), while the motor speed was maintained constant throughout a given series of experiments. All experiments were run at the temperatures and humidities of the laboratory, which ranged from 14.7° to 23.7° C. and from 46 to 80 % R.H. between experiments. All but a few experiments were carried out between 18° and 23° C. Temperatures were maintained constant to within 1.0° C. during any one experiment, and the insects were adapted to laboratory temperature and humidity for several hours before each series of experiments.

Measurement of wind speed

The hot-wire anemometer was used for speeds below 1.0 m./sec., and above this speed the Pitot tube was employed. The manometer attached to the latter was filled with chloroform and tilted so as to give a large-scale reading for a small pressure difference. The scale was calibrated by using a previously calibrated fan anemometer as a standard. The use of still air was avoided in order to guard against undesirable variations of temperature. A slow drift of air of about 0.05 m./sec. was therefore the minimum used during observations on activity. This speed could be measured readily with the hot-wire anemometer, and caused a deflexion of about 3 mm. on the meter used in the bridge circuit.

Insects at rest on the transparent sides of the insect chamber experienced smaller wind speeds than those measured by the anemometer in the centre of the wind channel. The average wind profile close to the surface is shown in Table 1 for the cross-section passing through the centre of the chamber. The measurements were obtained by using the hot-wire anemometer or Pitot tube as a probe. At low wind speeds the upper and lower surfaces of the thorax of a resting fly were respectively 0.5 and 0.25 cm. from the surface. The insects crouched closer to the surface at higher speeds. Most of the flies were therefore exposed to a gradient of wind speed ranging from that measured by the anemometer to a value about 30 % less, while a proportion immediately down-wind from the others were sheltered to a varying degree. The wind speeds quoted in the following experiments are for convenience the values measured by the anemometers in the usual position near the centre of the wind channel.

The range of nominal wind speed to which the flies were exposed covers that found in the field. Measurements of wind speed in vegetation are usually below 1.0 m./sec. and an insect at rest is rarely in a position where it is exposed to a wind so great as 8.0 m./sec.

Table 1. *Reduction of wind speed close to surfaces and corners of insect chamber for cross-section in middle of chamber*

Position	Wind speed (m./sec.)		
Centre of cross-section	0.5	4.5	8.0
From mid-points of surfaces	1.0 cm. from surface	0.50	4.4
	0.5 cm. from surface	0.49	4.1
	0.25 cm. from surface	0.39	3.4
From corners inwards at 45° from the surfaces	1.0 cm. from corner	0.5	4.3
	0.5 cm. from corner	0.45	3.8
	0.25 cm. from corner	—	3.3

Measurement of activity

Flight activity was assessed exactly as described previously (Digby, 1958), that is by counting the total number of short flights in 45 sec. out of every minute and reducing the figure to flights/specimen/min. On some occasions walking activity also was assessed towards the end of each minute period by counting the numbers which were walking continuously or with short rests of 1 or 2 sec., at the moment of observation. When more active, the numbers walking were estimated to the nearest five. The figures are expressed in this paper as the percentage of the population showing walking activity.

THE EFFECT OF WIND SPEED

Flight and walking activity

In order to study the relation of activity to wind, groups of flies were subjected to a convenient standard wind speed of 0.5 m./sec. for a period of 30 min. or longer, to ensure a reasonable degree of adaptation. The wind speed was then changed to a higher or lower value for a further period, after which it was returned to the standard speed once more. Three such experiments, shown in Figs. 1-3, illustrate the changes from 0.5 m./sec. to 3.0, to 8.0 and to 0.05 m./sec. The change to both higher and lower speeds resulted in reduction of flight activity. This was most strongly marked at the higher wind speeds, and here the decrease of flight activity which occurred when the wind speed was raised to a high value was followed by a partial recovery as the insects adapted to the higher level of stimulus. On return from the high value to the standard 0.5 m./sec. activity showed an immediate increase, the rate at first rising to a level much greater than that during the initial period at the standard wind speed, and then declining as adaptation occurred back to a level of activity appropriate to the 0.5 m./sec. speed. Adaptation effects were very slight at low wind speeds (Fig. 3).

Walking activity was affected by change of wind speed in a way closely parallel to flight activity. An estimate of the percentage walking during the change to 8.0 m./sec. and back again is shown in Fig. 2, the observations on walking and on flight activity being taken from two identical experiments. The change of activity due to the change of wind from 0.5 to 0.05 m./sec. and back (Fig. 3) was relatively

small and difficult to follow in these experiments where the flies were adapted to a wind of 0.5 m./sec.; but if they were adapted to still air and observed at a low light intensity the walking activity was much less and therefore more easy to follow, the effect of the change of wind speed being greatly enhanced. Fig. 4 shows one such

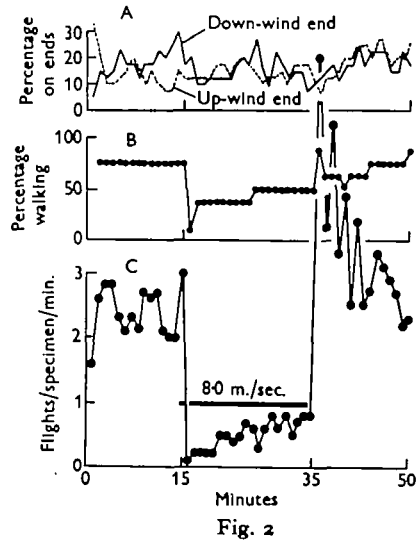
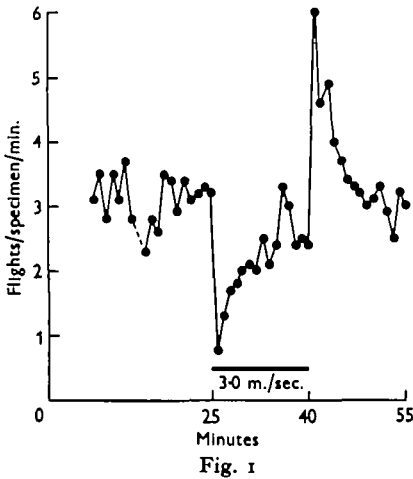


Fig. 1. Effect of change of wind speed from 0.5 to 3.0 m./sec. and back on mean flight activity of a group of forty flies.

Fig. 2. Effect of change of wind speed from 0.5 to 8.0 m./sec. on: A, percentage on up-wind end of insect chamber (dotted line) and down-wind end (continuous line); B, percentage walking; and C, flight activity. Data from two identical experiments.

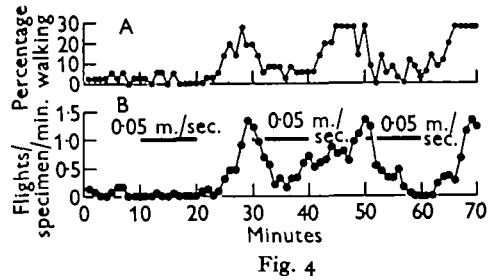
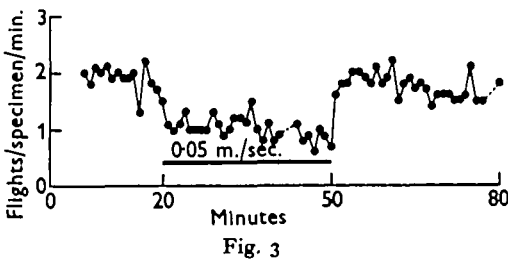


Fig. 3. Effect of change of wind speed from 0.5 to 0.05 m./sec. and back on flight activity.

Fig. 4. Effect of change of wind speed from 0.5 to 0.05 m./sec. on: A, walking activity; and B, flight activity in the same experiment. Run at low light intensity (2.0 instead of 160 lux).

experiment carried out at a light intensity of 2 lux with insects previously adapted to still-air conditions. It can be seen that there was a very close agreement between walking and flight activity.

Curves relating the change of flight activity to change of wind speed are shown in Fig. 5. The curves were produced from the results of ninety-four experiments,

similar to those of Figs. 1-3 but mostly of shorter duration, carried out at 160 lux. Flight activity for the periods of the first, the second to the fifth and in a few cases of the twenty-first to thirtieth minutes after the change of wind speed from 0.5 m./sec. is expressed as a percentage of that prevailing during the last 10 min. before the change. The distribution of the points shows that under these particular conditions the optimum wind speed for flight activity lies at about 0.7 m./sec. There was a considerable degree of adaptive recovery from the inhibiting effects of a continuing

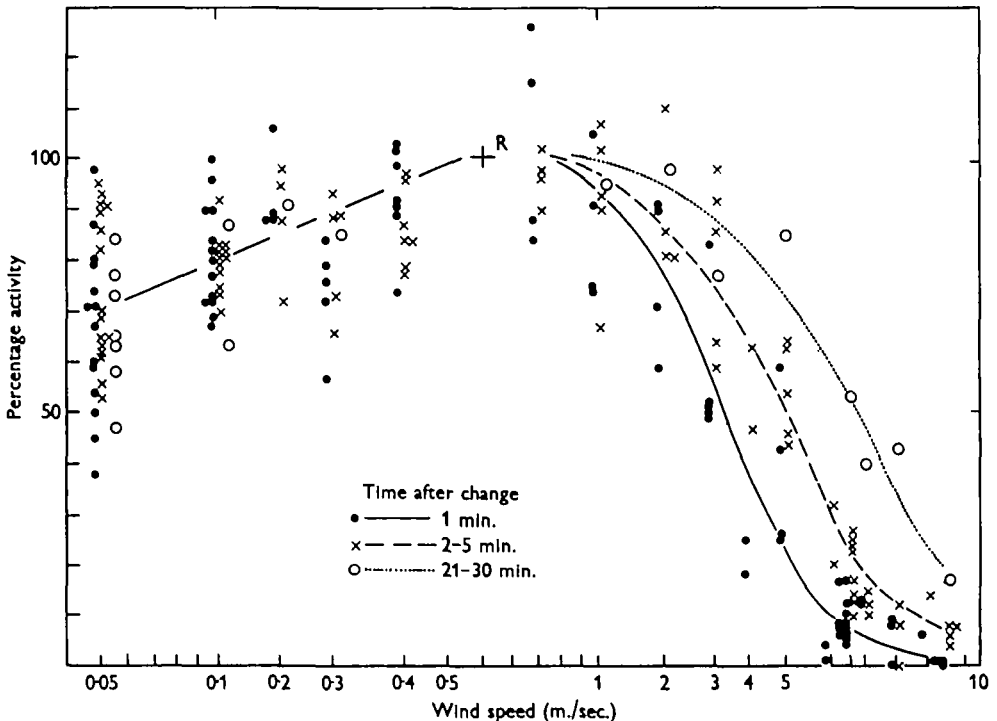


Fig. 5. Activity following a change of wind speed at various periods after the change. Activity expressed as a percentage of that prevailing during the last 10 min. of the preceding period at 0.5 m./sec. The point *R* is the reference point, 100 % at 0.5 m./sec.

high wind, but the adaptive changes which followed reduction of the wind speed from 0.5 m./sec. to lower values were almost negligible in these experiments. There was a considerable range in the degree of sensitivity to low wind speed. This sensitivity was readily lost after prolonged activity or prolonged exposure to a wind of 0.5 m./sec., or after a short exposure to a strong wind.

The temperatures and humidities at which these experiments were carried out ranged from 16.6° to 23.4° C. and from 46 to 80 % R.H. There was no significant correlation between these factors and activity change either above or below the optimum. Nor was there a significant correlation with the initial level of activity, which varied from 1.3 to 4.2 flights/specimen/min.

Mechanical effects of wind speed

The question arises to what extent the flight activity as observed reflects the true excitability of the population and to what extent it is modified by the insects either being blown off the surface or being unable to leave it. At the standard wind speed of 0.5 m./sec. the insects were distributed more or less at random and flights were made about the chamber in all directions. Observation suggested that at this speed and below it almost every flight was voluntary. Furthermore, when the wind speed was reduced to 0.05 m./sec., the proportion walking, and also the tempo of activity displayed in walking, decreased together with the flight activity (Fig. 4), showing the activating effect of a wind speed of 0.5 m./sec. to be a true activation and not a spurious effect arising from the insects being dislodged from the walls of the chamber by a stronger wind.

Above 0.5 m./sec. flight resulted in displacement down-wind more commonly than up-wind. At 4.5 m./sec. up-wind flights were still possible, but activity on the gauze at the down-wind end was restricted in the main to short hops of an inch or two. At this speed, all the members of the group appeared to be able to make short hops and flights, which could easily be seen and counted. It is therefore unlikely that mechanical inability to take to flight played any significant part in modifying flight activity at 4.5 m./sec. and observation suggested that nearly all the flights were still voluntary.

At the highest speed employed, 8.0 m./sec. (Fig. 2), the insects initially at rest or walking on the sides or on the up-wind end of the chamber were swept down-wind immediately they took to flight or left the surface. It was not possible to see whether all these flights were voluntary in origin, but the fact that walking and flight activity in normal flies was reduced almost to zero for a minute or two after increasing the wind to 8.0 m./sec. showed that the insects at rest were not swept off the surface by the force of the wind even at this speed. After the initial great reduction of activity the proportion walking, and the activity displayed in walking, increased again together with the flight activity. A part of the apparent flight activity during this period may well be due to the insects losing their footing whilst walking in the strong wind. Most of the flies on the down-wind end, usually about one-third of the total number in the chamber, were unable to make hops or flights away from the surface at this speed.

It may therefore be concluded that the changes in flight activity described in these experiments concern mainly activation or inhibition of flight activity up to 4.5 m./sec. and mechanical factors arising from the force of the wind play a part in modifying this activity at 8.0 m./sec.

The position of the population in the insect chamber

The effect of high wind speed on the distribution of the flies within the chamber is of significance to the estimation of flight activity, for the insects on the down-wind end could not make flights at 8.0 m./sec. The population of the whole, however,

remained fairly well distributed about the chamber in the face of very considerable changes of wind speed.

In these experiments when the flight activity was about 2.0 flights/specimen/min. roughly half the flies were in the walking phase of activity at 0.5 m./sec. The direction of walking, as of flying, was more or less random. When the wind speed was increased the numbers walking decreased; but a greater proportion of the insects became orientated into the wind. This resulted in their walking up-wind at a rate which tended to counteract the rate of down-wind movement of the population resulting from flight.

A count of the numbers on the down-wind end was taken as a measure of the extent to which these two movements balanced. Table 2 gives the results of 8 experiments in which the wind speed was changed from 0.5 m./sec. to a higher value for 15 min. or more. One of these is that shown in Fig. 2. Up-wind movement predominated when the wind was changed to 2.0 and to 4.5 m./sec. The two tendencies balanced remarkably well, and not more than 20% of the population was found on the down-wind end at the speed of 8.0 m./sec. at which flight activity was limited for mechanical reasons.

Table 2. *Normal flies; proportion on down-wind end of insect chamber after change of wind speed from 0.5 m./sec. to higher values*

Exp. no.	Higher value of wind speed	Percentage on down-wind end						
		During last 10 min. of initial period at 0.5 m./sec.	During following periods after change to higher value (min.)					
			1-5	6-10	11-15	16-20	21-25	26-30
1	8.0	27	15	11	16	19	11	6
2	8.0	20	18	9	17	16	—	—
3	8.0	20	13	16	19	12	—	—
4	6.5	20	24	23	31	41	40	39
5	4.5	19	22	25	22	22	—	—
6	4.5	20	29	32	36	33	—	—
7	2.0	15	32	18	20	19	—	—
8	2.0	22	25	33	37	—	—	—

THE ANALYSIS OF ADAPTATION TO WIND

The range of wind speed from 0.5 to 4.5 m./sec., in which an increase of wind speed decreases activity

Adaptation effects were prominent in the relation of activity to wind above 0.5 m./sec. Analysis of adaptation to higher and to lower wind speeds was carried out in the range from 0.5 to 4.5 m./sec. This range was notable for the powerful inhibition produced by a strong wind; the small activating effect included may be neglected.

The methods used were those described for studying adaptation to change of light intensity (Digby, 1958). The principle is that the extent of rebound during the first minute after a period at a different level of stimulus may be taken as a measure of

the amount of adaptation to it. Two sets of experiments were carried out. In the first set (Fig. 6) an initial observation of activity was made over the last 10 min. of a period of $\frac{1}{2}$ hr. or more at 0.5 m./sec.; the wind speed was then changed to 4.5 m./sec. for a period which was varied in successive experiments and lastly was returned to 0.5 m./sec. Observations of activity were made in this second period at 0.5 m./sec., the activity being expressed as a percentage of that during the last 10 min. of the initial period at this speed. The recovery curves correspond to the continuous line of the inset graph (Fig. 6). They show the time course of the adaptive decline of activity which followed the immediate peak caused by the cessation of inhibition due to the high wind speed. The distance of the initial

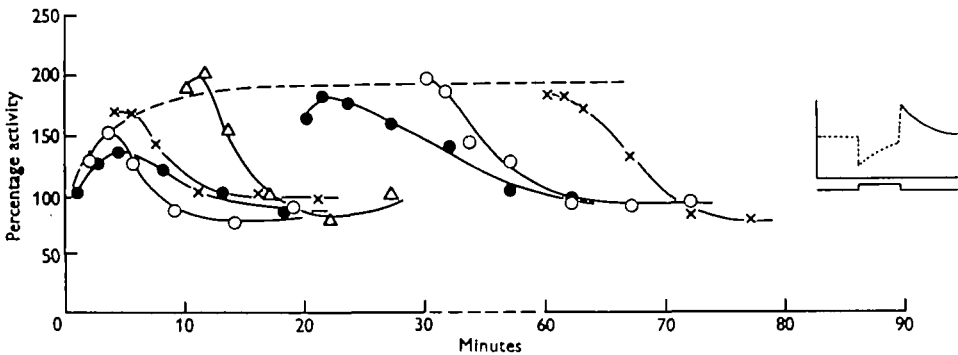


Fig. 6. Higher wind range; adaptation to high wind speed (i.e. family of recovery curves at 0.5 m./sec. after varied periods at 4.5 m./sec. during which the activity was much less; see inset graph). The broken line passing through the initial point of each recovery curve shows the time course of adaptation to 4.5 m./sec. Activity expressed as a percentage of that prevailing during the last 10 min. of the initial period at 0.5 m./sec., time as minutes elapsed since the end of this initial period.

point of each recovery curve along the time scale marks the duration of the preceding period of high wind speed. The initial points of the recovery curves depart from the 100% level by an amount which is a measure of the amount of adaptation to the 4.5 m./sec. wind speed at that instant, and the broken line passing through the initial points indicates the course of this adaptation in relation to time. This curve is diagrammatic since, as in the case of those shown for adaptation to light, the population varied somewhat in sensitivity between the experiments.

In the second series of experiments (Fig. 7) the changes were carried out with the wind velocities in the reverse order, the family of recovery curves at 4.5 m./sec. being observed after a period at the lower wind speed during which the activity had been much greater. These curves show the adaptive increase of activity which followed the immediate depression resulting from resumption of the high wind speed. In this case the departure of the initial point of each recovery curve from the initial level of activity is a measure of the extent of adaptation to the lower wind speed, and the broken line indicates the course of adaptation to the lower wind speed in relation to time.

These two sets of curves show that a longer period of adaptation was followed by a slower recovery from the subsequent rebound and that adaptation to both the higher and the lower wind reached a maximum after 10–20 min. The one set of curves bears a close resemblance to the other set inverted, the increase of activity following the release of inhibition (Fig. 6) being nearly as sharp as the decrease of activity which occurred when the inhibition was applied (Fig. 7). In this there is a striking contrast to the adaptation phenomena described for increase and decrease in light intensity, where the increase of activity was delayed by the persistence of a state of low activity. A trace of the same phenomenon can be seen here, however, in that the peak of activity following the removal of inhibition by a 4.5 m./sec. wind (Fig. 6) is reached in the earlier curves not in the first minute after the change, but in the second to third minutes after.

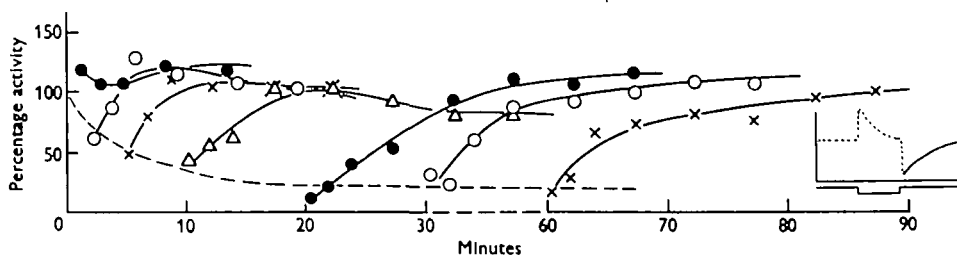


Fig. 7. Higher wind range; adaptation to low wind speed (i.e. family of recovery curves at 4.5 m./sec. after varied periods at 0.5 m./sec. during which activity was much greater; see inset graph). The broken line passing through the initial point of each recovery curve shows the time course of adaptation to 0.5 m./sec. Activity expressed as a percentage of that prevailing during the last 10 min. of the initial period at 4.5 m./sec., time as minutes elapsed since the end of this initial period.

*The range from 0.05 to 0.5 m./sec., in which an increase of
wind speed increases activity*

Comparable experiments were carried out in this range. Recovery curves at 0.05 m./sec. after periods of up to 1 hr. at 0.5 m./sec. were all very similar, showing activity to decline to the level appropriate to the lower wind speed during the first minute and then to remain steady as in Fig. 3. The lack of subsequent recovery can be seen in Figs. 3 and 5.

In contrast, recovery curves at 0.5 m./sec. after various periods at 0.05 m./sec. (Fig. 8) all show a much slower increase of activity up to the level appropriate to the 0.5 m./sec. wind, taking more than 10 min. to obtain a steady value after an hour at the lower wind speed. As before, the longer the initial period at 0.05 m./sec., the slower the recovery. These curves are superficially similar to those obtained at 4.5 m./sec. after varied periods at 0.5 m./sec. (Fig. 7), but this similarity is only superficial since in the latter case the curves are those of recovery from an immediate rebound from a much higher level of activity occurring during the previous period at the lower wind speed. The recovery curves after varied periods in still air are more comparable to those following an increase of stimulation by light intensity (Digby, 1958, Fig. 7), showing the same slow recovery from a state of low activity.

The wind-adaptation curves differ from the light-adaptation curves in the absence of a conspicuous early peak of high activity, suggesting that adaptation to the stimulus of wind was much less than that to light at the values employed.

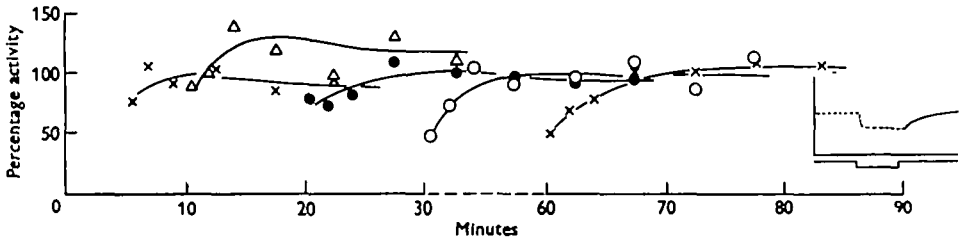


Fig. 8. Lower wind speed range; recovery curves at 0.5 m./sec. after varied periods at 0.05 m./sec., during which activity was less (see inset graph).

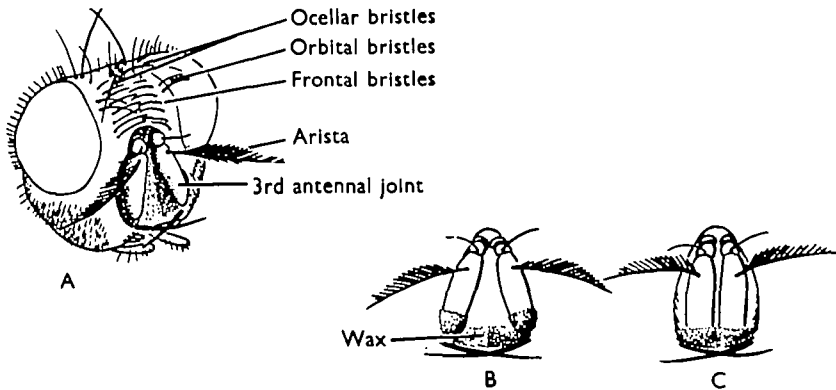


Fig. 9. Head of *Calliphora*. A, Normal fly, ♀; B, facial depression and antennae, waxed as control to experiments in which antennae immobilized; C, antennae immobilized by waxing to facial depression.

THE COMPONENTS OF THE REACTIONS TO CHANGE OF WIND SPEED

The inhibiting effect of antennal movement

The occurrence of an optimum wind speed with a decline of activity at higher and at lower speeds suggested that there might be at least two antagonistic reactions involved.

It is convenient to consider first the inhibition of activity to wind shown by normal flies above the optimum speed. A current of air causes movements of the antennae and of the numerous bristles distributed about the head and other parts of the insect. Each antenna consists of two short basal joints and an elongate third joint, which may lie vertically in the facial depression, or may be held out obliquely forwards (Fig. 9). This third joint bears a prominent plumose bristle, the arista. A current of air of about 0.5 m./sec. from the front of the insect moves the arista relative to the third joint to a rather limited degree, and it moves the third joint relative to the head, rotating it about its long axis. In stronger winds the third

antennal joint is deflected upwards and outwards. At the base of each antenna is a sense organ, Johnston's organ, situated in such a position as to suggest an ability to appreciate movements of the antennae. As the antennae are known to be concerned in flight reflexes (Hollick, 1940) it seemed reasonable first to investigate this organ.

In a series of experiments, details of which are given in Table 3, the two third antennal joints of each member of groups of forty flies were fastened into the facial depression with wax (Fig. 9), applied with an electrically heated loop of wire while

Table 3. *Effect of change of wind speed from 0.5 to 4.5 m./sec. on activity of flies with antennae immobilized*

(This change produces inhibition in normal flies.)

Exp. no.	Light intensity (lux)	Activity during preceding 5 min. at 0.5 m./sec. for each trial (flights/specimen/min.)	Effect of change of wind 0.5-4.5 m./sec. O, no effect; A, activation	
			On flight activity	On percentage walking
1	2600	2.62	O	O
		2.84	O	A
		2.20	O	A
2	2600	1.30	O	—
		1.28	O	—
		1.10	O	—
		1.16	O	—
		1.16	O	—
3	2600	1.27	O	A
		0.87	A	A
		0.17	A	A
4	2600	0.86	O	—
		1.24	O	—
		1.16	O	—
5	2600	0.56	O	A
		0.23	A	A
6	2600	0.53	O	A
		<0.08	A	A
		<0.03	A	A
7	160	1.52	O	O
		1.00	O	O
		0.74	O	O
8	2.0	0.65	A	A
		0.34	A	A
		0.64	A	A
9	160	0.43	A	—
		0.22	A	A
		0.22	A	A
10	2.0	0.22	A	A
		0.08	A	A
11	20.0	0.12	A	A
		0.13	A	A
		0.21	A	A
12	2.0	0.06	A	A
		0.02	A	A
		0.03	O	A

the insects were anaesthetized with a mixture of chloroform and ether. After recovery they were tested for the effect of the change of wind speed from 0.5 to 4.5 m./sec. Each experiment consisted of an initial acclimatization period of 10 or 20 min. at 0.5 m./sec. followed by alternate periods of 10 or 15 min. at 4.5 and 0.5 m./sec., each change from 0.5 m./sec. to the higher value constituting a trial. Each experiment was normally accompanied by a similar control run with previously anaesthetized but otherwise normal flies. Fastening the antennae to the head was found to abolish completely the inhibiting effect of a wind of 4.5 m./sec. (Fig. 10) and, when the activity was low, activation appeared instead (Fig. 11, Table 3). This operation also reduced the activity at 0.5 m./sec. by about one half, but the presence or absence of inhibition by a high wind was not related to the level of activity.

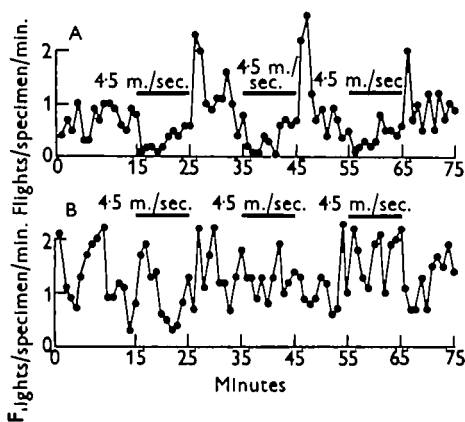


Fig. 10

Fig. 10. Effect of immobilizing antennae on reaction to change of wind from 0.5 to 4.5 m./sec. A, Control group, antennae waxed but not immobilized; B, experimental group with antennae immobilized.

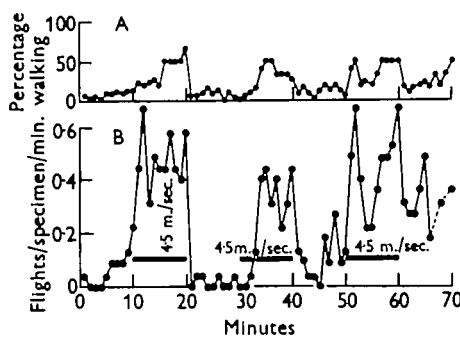


Fig. 11

Fig. 11. Effect of immobilizing antennae on reaction to change of wind from 0.5 to 4.5 m./sec. at low light intensity (2.0 lux). A, Walking activity; B, flight activity from same experiment.

In order to separate the possible effect of waxing the facial depression and antennae from the effect of immobilizing the antennae, the flies in four of the control groups, each numbering thirty or forty individuals, were waxed as in the experimental groups but the antennae were left freely mobile. A total of eleven trials with these groups showed a reduction of activity in a 4.5 m./sec. wind very similar to that shown by normal insects.

The arista is carried on the third antennal joint and as this projects into the air stream it seemed likely that much of the movement of the third joint might be due to deflexion of the arista by the wind. Amputation of the arista close to the base in each member of groups of twenty and thirty-three flies, without waxing down the antennae, had however a negligible effect, the population exhibiting a reduction of activity very similar to that of normal flies when subjected to a wind of 4.5 m./sec. Observation of single flies showed that amputation of the arista had in fact relatively

little effect on the upward and outward movement of the third joint of the antenna in a strong wind, although it abolished the slight rotation imparted by the arista at lower wind speeds. The arista therefore has little influence on the inhibiting effect of a 4.5 m./sec. wind.

Table 4. *Flies with antennae immobilized; proportion on down-wind end of insect chamber after change of wind speed from 0.5 to 8.0 m./sec.*

(Average of 8 exps.)

Percentage on down-wind end			
During last 10 min. of initial period at 0.5 m./sec.	During following periods after change to higher value (min.)		
	1-5	6-10	11-15
19	32	23	21

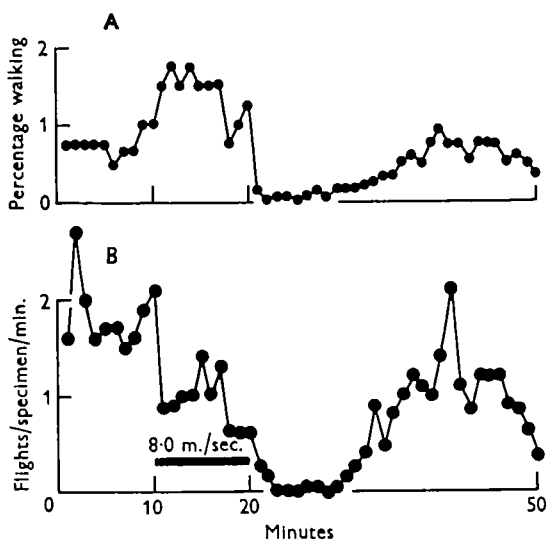


Fig. 12. Flies with antennae immobilized; effect of change of wind speed from 0.5 to 8.0 m./sec. and back. A, Walking activity; B, flight activity.

When these insects with the antennae immobilized were subjected to a wind speed of 8.0 m./sec. for 5 or 10 min., a reduction of flight activity still occurred in five out of ten experiments. Some flight activity was, however, obviously prevented from appearing at 8.0 m./sec. by the mechanical inability of the flies on the down-wind end to make recognizable flights. This mechanical effect was initially rather greater in flies with the antennae immobilized than in normal flies, because in the former an increase of wind from 0.5 to 8.0 m./sec. caused a down-wind movement during the first 5 min., from which there was a recovery (Table 4), complete by 11-15 min. after the change to the higher wind speed. The increase of walking activity during the period at high wind speed (Fig. 12) showed that in these insects activity in fact increased at 8.0 m./sec.

We may therefore conclude that the greater part of the inhibiting effect of the changes of wind speed from 0.5 to 4.5 and to 8.0 m./sec. resulted from movement of the third antennal joint relative to the head.

Activation

In normal flies, so long as they had not previously been rendered insensitive, the stimulus of wind at speeds below 0.5 m./sec. caused activation (Figs. 3-5). The same effect occurred at higher speeds when the antennae had been immobilized with wax and the initial activity of the insect was low. It can be seen from the experiments listed in Table 3 that the upper limit of initial activity for the appearance of activation by the change of wind from 0.5 to 4.5 m./sec. was about 0.5 flight/specimen/min. For this reason the stimulating effect of wind appeared more commonly at low light intensities (Table 3, Exps. 7-12). It also appeared in these operated insects when they were torpid immediately after recovery from anaesthesia or after the halteres had been fixed down with wax. This increase of activity at 4.5 m./sec. in flies with immobilized antennae might be considered to be a spurious effect arising from an increased number losing their footing when relatively torpid. This was shown not to be the case by the fact that the numbers walking also increased at the higher wind speed (Fig. 11).

The absence of activation by a wind of 4.5 m./sec. in these operated flies when the initial activity was above a certain level was comparable to its absence at 0.5 m./sec. in normal flies after prolonged flight or exposure to strong wind. This suggests that when the insects were active their own movements ensured sufficient adaptation to the wind for them not to react to it. The increase of walking amongst the antennae-immobilized flies at 8.0 m./sec was not restricted to groups with an initial low level of activity.

The activating effect of wind was therefore present at all speeds, although in normal insects its appearance in a strong wind was suppressed by the more powerful inhibition.

Experiments were carried out to assess to what extent the large bristles on the head might be responsible for activation.

The structure of the head of *Calliphora* is very similar to that of *Muscina stabulans*; Hollick (1940) found that *Muscina* when attached to a support would carry out flight movements after the antennae had been immobilized but not after the head have been covered with a celloidin capsule. These results suggested that in the latter case receptors other than the antennae may be affected (Chadwick, 1953). The front of the head bears a number of prominent bristles (Fig. 9) and experiments were therefore carried out to see if these might be responsible for the activation. Although the facial bristles and vibrissae move very little, the arista and the frontals and orbitals are all deflected by a slight wind. These latter groups (that is the arista and the frontals and orbitals, together with the single large bristle borne on each second antennal joint) were therefore amputated from a number of specimens of *Calliphora* by clipping them off as close to the base as possible under chloroform-ether anaesthesia, while the flies were held by the wing to avoid damaging the other

bristles left intact. When attached to a support in the wind tunnel, flight movements were still possible in both males and females, although they occurred rather less readily than in normal flies.

When free in the insect chamber, *Calliphora* only became obviously orientated into the wind at speeds of 4.5 m./sec. and above, but it seemed likely that if the sensitivity to wind were strictly localized, the bristles on the head might yet be those mainly concerned. In a series of experiments, these same bristles were amputated from groups of twenty to forty flies which were then tested for the effect of the change of wind speed on flight and walking activity, each experiment consisting of three repeated changes of wind speed from 0.5 to 0.05 m./sec. Each experiment was accompanied by a control using flies which had previously been anaesthetized but not operated upon.

Six out of eight experiments following removal of these bristles still showed activation by the higher wind speed. The flies used for these were comparable to those in the other experiments described in this paper in that they had been moderately active for some days before these observations. In the remaining two experiments the activating effect was abolished and inhibition took its place. These two experiments were carried out with flies which had been kept under quiet conditions in the breeding cages for 2 or 3 weeks prior to the experiments. Although insufficient to define closely the conditions under which the head bristles are important, these experiments sufficed to show that while these bristles may sometimes contribute to the activating effect of wind, they were not the only organs or mechanism concerned.

The reduction of activity following exposure to strong wind

When a population of normal flies was subjected to an increase of wind from 0.5 m./sec. to a higher value, activity was immediately depressed and then increased as the flies adapted to the new conditions. In a certain number of cases this increase of activity was not maintained and activity declined again after a while. In all cases, however, the resumption of the low wind led to the rebound to a high level of activity as in Figs. 1 and 2.

When the same experiment was carried out with flies in which inhibition was suppressed by immobilization of the antennae, the depressing effect of a wind of 8.0 m./sec. was more obvious, setting in from the first few minutes of the period at high wind speed. Return to low wind speed resulted in a further immediate fall in flight and walking activity, followed by a slow rise (Fig. 12). The occurrence of these effects is set out in Table 5.

A family of curves for the subsequent depression of activity at 0.5 m./sec. in flies with the antennae immobilized is given in Fig. 13, flight activity being expressed as a percentage of that at 0.5 m./sec. before the period of high wind speed. These curves show that the depression was greater and lasted longer following longer periods at 8.0 m./sec.

The post-inhibitory rebound to high activity shown by normal flies was therefore a dominant rebound superimposed upon an activity curve of this nature, arising from some other effect of the wind. The fact that normal flies and those with the antennae

Table 5. Occurrence of reduction of activity after prolonged exposure to high wind speed in normal flies and in flies with antennae immobilized

	Wind speed (m./sec.)	No. of experiments in which winds maintained at high value for 20 min. or more	No. of experiments in which depressing effect of wind begins during period at high wind	Activity shown when 0.5 m./sec. wind speed resumed
Normal flies	8 6 5 4.5 2	4 1 1 16 1	2 } (depressing effect sets in 10-20 min. after onset of high wind) 0 1 4 1	Rebound to high level of activity
Flies with antennae immobilized	8	4 Exps. with winds at high value for 15 min. or more	4 (effect sets in during first few min.)	Further fall in activity (9 expts.)

waxed but not immobilized became very active after exposure to a high wind showed that flight was not limited by the wind having caused undue fatigue or injury. It seems likely that the low activity was largely a rebound from excessive activation by the high wind. The fact, however, that the rebound was so large compared with the apparent magnitude of the activating effect, and that the depression of activity set in during the period at high wind speed, suggests that additional factors may have been involved.

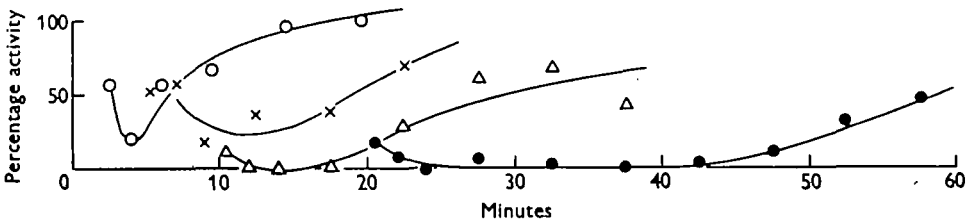


Fig. 13. Flies with antennae immobilized; recovery curves at 0.5 m./sec. following varied periods at 8.0 m./sec.

DISCUSSION

The effect of change of wind speed

The experiments of Davies (1936) and Haine (1955*a, b*) have shown that wind causes inhibition of flight in aphids. No laboratory investigations so far appear to indicate that wind increases the numbers of insects taking to flight, although stimulation by wind has been shown to play a part in the initiation and maintenance of flight in *Muscina* (Hollick, 1940) and in locusts (Weis-Fogh, 1949, 1956). The present results have shown that wind can cause an increase or a decrease of activity in *Calliphora* according to the range of wind speed, the optimum being at about

0.7 m./sec. under the particular experimental conditions. The differences in adaptive changes in activity following changes of wind at lower and at higher speeds provide an interesting contrast between a reaction in which inhibition is not important, and one in which it is dominant. In the low wind speed range from still air to 0.5 m./sec. in which wind has an activating effect and inhibition is very slight, a decrease of wind causes an immediate decrease of activity without subsequent recovery, and an increase causes a more or less gradual increase of activity. The state of low activity tends to persist as in recovery from low light intensity (Digby, 1958). In the higher wind speed range where inhibition is involved, both increase and decrease of wind speed cause a sharp response which is followed by a considerable degree of adaptive recovery over a period of 20 min. or more.

The nature of the reactions to wind

It has been shown that the effect of wind speed is complex. There is an activating effect from the lowest speeds to the highest; there is an over-riding inhibitory effect with the threshold at about 0.7 m./sec.; and there is a further depressing effect of prolonged high wind. It has been possible to show that under some conditions the bristles of the head account for a large part of the activating effect, but in previously active flies their effect is negligible. It has also been possible to show that the inhibiting effect of strong wind arises from movement of the third antennal joint.

The extent to which the activation and inhibition of walking and flight activity may be related to the reflex mechanisms of initiation and maintenance of flight (see Pringle, 1957) is uncertain, although it seems likely that there may be some parallel. For instance, the small activating effect of wind on the bristles of the head is comparable to its effect on flight activity in the mounted insect.

Conditions are not, however, strictly comparable in the two cases. Thus when flies are at rest on a surface a strong wind has an activating effect which is normally suppressed by the inhibiting action of the antennae; it does not necessarily follow that the activating component occurs in insects in which the air-flow arises by virtue of their own flight, because it may well arise in some way from the stresses imparted by the insects clinging to the surface. Movement of the third antennal joint of *Muscina* was shown by Hollick (1940) to affect the path of the wing-tip during flight and to cause the reflex lifting of the legs when a jet of air was directed at the head. These reflexes are of obvious importance in flight, but it is difficult to see what part the inhibiting effect of movement of the third antennal joint of *Calliphora*, described in the present paper, might play in flight itself. During flight in a mounted insect the third joint vibrates rapidly, and it seems probable that it may then produce an even more powerful inhibiting stimulus than in an insect at rest. If so, it may perhaps serve to balance in some way the activating stimuli arising from other sources during flight. It would follow that after each flight a normal fly would experience a rebound to a state of higher excitation than would a fly with the antennae immobilized. That such may be the case is supported by the

fact that immobilizing the antennae reduced the number of flights compared with those made by normal controls, although the actual flights made by the insects with immobilized antennae were apparently normal.

Ecological significance

Lack of sufficiently detailed field studies on the reactions of *Calliphora* or other dipterous flies to wind speed so far precludes comparison of these laboratory experiments with field behaviour. These experiments do, however, suggest the type of behaviour which is likely to occur in the field. Under the experimental conditions activity increased with wind speed up to about 0.7 m./sec. and decreased with increase of wind above this speed. The optimum speed probably varies with many factors, but nevertheless the experimental figure of about 0.7 m./sec. is above the range of wind speed usually found under the microclimatic conditions experienced by an insect at rest. So far as this optimum prevails in the field an increase of wind speed alone may be expected to increase activity in sheltered situations, in vegetation and close to the ground, and to decrease it in exposed situations. The activating effect of a low wind speed in the field is likely to be much greater than is indicated in these experiments, as the insects are probably adapted to still air conditions to a much greater degree, and this would enhance the effect. Wind in the field is normally turbulent, and in more exposed situations where speeds above the optimum prevail the inhibition of activity by wind would tend to result in reduced activity during gusts and increased activity during lulls. The occurrence of a rebound from the inhibition by wind would tend to allow a maximum amount of activity during windy weather for a minimum amount of displacement of the population by wind.

It is to be noted that under sunny conditions in the field the activating and inhibiting effect of wind is likely to be complicated by the results of substantial changes of temperature arising from heat loss by convection, variation of which is particularly great at the low speeds prevailing under microclimatic conditions (Digby, 1955). The effect of wind by itself is to be sought under overcast conditions.

Field observations of locusts (Strelnikov, 1936; Kennedy, 1939; Waloff & Rainey, 1951; Rainey *et al.* 1957) have suggested that very similar reactions may occur in these insects. Thus the first downward movements made by roosting locusts early in the morning appear to be partly stimulated by light gusts of wind which therefore have an activating effect. These insects have been quiescent during the night; later in the day when they become more active flight is inhibited by moderate winds and under gusty conditions they take to flight during the lulls and land during the gusts. In strong winds they remain on the ground and walk up-wind. Although there are great differences between the structure and ecology of *Calliphora* and these locusts, it is interesting that the field behaviour of the locusts in these respects agrees with that to be expected of *Calliphora* from the experiments described in this paper.

SUMMARY

1. A study has been made of the effect of wind speed on the flight activity of a population of the blowfly *Calliphora erythrocephala* in a small wind tunnel.
2. Under the experimental conditions wind has an activating effect up to about 0.7 m./sec., above which it inhibits flight.
3. Below 0.5 m./sec., activity decreases rapidly with decrease of wind speed and then remains at or close to the lower value. The increase of activity arising from increase of wind speed is much slower, the state of low activity tending to persist.
4. At speeds between 0.5 and 4.5 m./sec. the changes of activity in response to both increase and decrease of wind are very rapid and are followed by a considerable degree of adaptation in each case.
5. Inhibition of activity by the change of wind speed from 0.5 to 4.5 m./sec. and to 8.0 m./sec. results from the movement of the third antennal joint relative to the head.
6. When this antennal movement is prevented, the change to 4.5 m./sec. causes activation if the initial activity is low, and the change to 8.0 m./sec. causes an increase of walking activity although flight is decreased for mechanical reasons.
7. Exposure to the higher speeds causes an additional depression of activity not dependent on movement of the third antennal joint.

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