FACTORS AFFECTING THE TEMPERATURE EXCESS 
OF INSECTS IN SUNSHINE 

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(1) INTRODUCTION 

The temperature of an insect is of paramount importance in determining its activity. 
When heated by the sun its temperature is not the same as that of the air but is 
greater by an amount which we will call the temperature excess. As activity is so 
dependent on temperature it is of considerable interest to know more about the way 
in which the various factors operate to control this temperature excess. 

The direct field observations so far made on the temperature excess of an insect 
in the sunshine apply to large forms such as the locust (Buxton, 1924; Strelnikov, 
1936; Kennedy, 1939; Gunn, Perry, Seymour, Telford, Wright & Yeo, 1948; 
Parry, 1951). Calculations such as those by Parry (1951), although they yield quite 
a reasonable answer for an insect the size of a locust at a considerable wind speed, 
involve a number of assumptions. There is reason to believe that certain of these 
would not hold good for most insects of temperate lands which are much smaller, 
and which are found when resting in positions with very low wind velocities. These 
wind velocities are certainly below 1 m./sec. and often below 0.1 m./sec. (see 
Stocker, 1928; Geiger, 1950). 

This paper describes laboratory experiments on the temperature excess of 
insects and plasticine spheres carried out under known conditions similar to those 
found in microclimatic conditions in the field, with a view to finding the temperature 
excess to be expected under natural conditions, and to elucidating the way in which 
the factors work at small size and low wind speed. 

Now it can be shown that for a small physical body similar to an insect the 
temperature excess varies directly with the radiation strength; with the absorptivity 
(which depends on the spectral composition of the radiation and on the 
colour and characteristics of the body); with a fractional power of the size, and 
 inversely with a fractional power of the wind velocity. Metabolism and evaporation 
are practically negligible in the resting insect. Uncertainty arises concerning the 
relations between temperature, wind and size, for at small size and low wind speeds 
 bodies tend to develop their own convection currents and to be controlled by the 
laws of natural convection rather than forced convection. It is to be expected that 
small insects in their natural habitat lie in the region of transition between these two 
types of flow. Of the factors involved in heat loss by convection, variation in the 
viscosity, density and conductivity of the air may be neglected as their effects over
the normal range of climatic variation are slight. Long-wave radiation between the insect and the background is also small and may be neglected. The main questions which we must consider for a representative range of insects are (i) whether temperature excess varies directly as radiation strength, or whether there are other complicating factors; (ii) what is the range of absorptivity; (iii) to what power of the size the temperature excess may be related, the 0.2 or 0.4 powers being characteristic of natural or forced convection respectively; and over what size range the powers hold good (see Appendix); (iv) to what extent temperature excess is dependent on wind velocity (natural or forced convection); and (v) whether the known heating effects of metabolic activity cause a temperature rise in a way which is strictly additive to that produced by radiative heat gain.

(2) METHODS

(i) The wind tunnel

A return-flow wind tunnel (Fig. 1), similar to that used by Ramsay (1935), was constructed, and the insect under observation was mounted facing the flow of wind in the centre of the air stream. Wind speeds in the 10–100 cm./sec. range were obtained by the use of a shunt channel and appropriate shutters to by-pass air from the insect channel. The armature and field of the fan were connected up in the manner used by Hollick (1940) to maintain a steady flow at low velocities. The experiments considered here were all carried out with the air temperature close to, or a few degrees above, that of the laboratory.

Wind velocity was measured by a hot wire anemometer, the element being a 1 cm. length of s.w.g. 50 platinum wire. Off-balance deflexion of the bridge galvanometer

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Fig. 1. Return-flow wind tunnel for determination of temperature of mounted insects under known conditions. Broad arrows indicate direction of air flow.
Factors affecting the temperature excess of insects in sunshine

was calibrated outside the tunnel against a smoke puff in a celluloid tube 1 or 2 m. long.

Radiation was provided by a 2 kW. Siemens projector bulb supported above the insect chamber by an arrangement so that it could be raised or lowered at will. The bulb, although rated at 240 V., was under-run at 210 V. to lengthen its life. Metal screens were used to cut off the long-wave radiation from the glass globe not immediately in line with the filament. A trough containing water or copper chloride solution was placed beneath the bulb, between it and the insect chamber, if desired.

(ii) Radiation measurements

A compensation instrument (Fig. 2) of the type of the Ångström Pyrheliometer (Ångström, 1899), was constructed for these measurements. The surfaces which received the radiation were two identical strips of manganin, each about 3 cm. long, and blackened with soot. Insulated thermocouples attached to the centre of each strip by a flake of mica were connected up to a galvanometer in such a way that any difference in temperature of the two strips produced a deflexion. In order to measure a given radiation, a shutter was moved so that one strip was exposed to the unknown radiation, while the other was heated by an electric current. The current

![Diagram of a pyrheliometer](image)

was adjusted until the two strips were of equal temperature, when the radiation strength was derived from the ammeter reading and an appropriate constant, itself derived from the area of the strips and their resistance, assuming the blackened surface to absorb 95% of the radiation irrespective of wave-length.

This particular instrument was constructed to have a large acceptance angle so that it would give an accurate reading when the bulb was close to the strips, and it was of such a shape that it could be placed inside the insect chamber with the blackened strips occupying the position in which the insect was later placed. It was checked against a Michelson actinometer obtained on loan from Kew Observatory, and which Dr G. Robinson had kindly calibrated against one of the Kew Ångström instruments.
Radiation intensity was usually adjusted by varying the height of the bulb, because it is not easy to use filters for reducing radiation which includes infra-red as well as visible without altering the spectral distribution at the same time.

Radiation conditions near the ground are complicated; they have recently been reviewed by Geiger (1950) and Sutton (1953). The most important component, the direct solar radiation, is received from the sun itself and from the small area of sky immediately round about. When the sun is high and the sky clear this may reach a value of up to 1.5 cal./cm.²/min. normal to the surface of measurement (Kimball & Hand, 1936; and see recent Kew values in Stagg, 1950). It is the equivalent of this component which was used in these experiments. Reflection and long-wave radiation were minimized by surrounding the insect by a black painted insect chamber maintained close to air temperature.

As absorptivity varies with spectral composition, it was necessary to insure that the spectral composition of the radiation used approximated to sunshine. The composition of the direct solar radiation for Washington and Davos, together with that of the radiation used in the experiments is shown in Table 1. The Washington figures are derived from a diagram published by Brackett (1936), itself derived from data by Abbot (1929), the curve taken being that corresponding to air mass 2. The Davos figures are those published by Sutton (1953) for the month of June. Measurements of spectral composition of the light from the bulb after it had passed through the water or CuCl₂ solution were made with the pyrheliometer in conjunction with the Chance filters On 20, OY 2 and OR 1, cut-off values being taken from published transmission curves. A depth of 2 cm. N/10 CuCl₂ gave a spectral composition close to that of Davos sunshine and a 2 cm. N/20 CuCl₂ a composition close to that of Washington sunshine. These depths of CuCl₂ had the disadvantage that they intercepted so much heat that a strength of 1.5 cal./cm.²/min. could not be attained in the insect chamber. For this reason, and as subsequent work showed that the spectral composition was of minor importance, a 3.5 cm. depth of water was used. Strictly, this gave a radiation more akin to Washington sunshine with a low sun, air mass 10 (where of course it is associated with a low total intensity).

Table 1. Percentage spectral composition of sun’s radiation at Davos and at Washington, and of the bulb with the various filter baths used in experiments

<table>
<thead>
<tr>
<th></th>
<th>Blue</th>
<th>Yellow</th>
<th>Red</th>
<th>Infra-red</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunshine at Davos, June</td>
<td>Under 0:56 μ 20.1</td>
<td>0:56-0:63 μ 11.9</td>
<td>0:63-0:76 μ 17.7</td>
<td>Over 0:76 μ 41.2</td>
</tr>
<tr>
<td>Sunshine at Washington (average air-mass 2)</td>
<td>Under 0:55 μ 12.9</td>
<td>0:55-0:64 μ 26.8</td>
<td>0:64-0:8 μ 15.4</td>
<td>Above 0:8 μ 44.5</td>
</tr>
<tr>
<td>Bulb plus 3.5 cm. water</td>
<td>11:1</td>
<td>12:2</td>
<td>25:8</td>
<td>51:0</td>
</tr>
<tr>
<td>Bulb plus 2 cm. N/20 CuCl</td>
<td>15:2</td>
<td>17:1</td>
<td>19:0</td>
<td>48:7*</td>
</tr>
<tr>
<td>Bulb plus 2 cm. N/10 CuCl</td>
<td>22:9</td>
<td>24:4</td>
<td>15:3</td>
<td>37:6†</td>
</tr>
</tbody>
</table>

* Nearest Washington. † Nearest Davos.
(iii) **Measurement of the temperature of an insect by a thermocouple**

The thermocouple units used for measuring the temperature excess consisted of two soldered eureka-platinum junctions of s.w.g. 50 wire connected to copper leads passing down a tube which supported the wire to which the insect was attached by soft wax (Fig. 3). In use, one of the junctions was inserted into the thorax of a heavily etherized or recently killed insect so as to lie in approximately the centre, between the muscle bands, and was sealed in position with a small drop of wax, while the other projected forwards into the air stream. These two junctions therefore measured the difference between the temperatures of the thorax and of the air stream. Temperatures are by no means uniform throughout an insect; in Table 2 is

![Diagram of thermocouple attachment to insect](image)

**Fig. 3.** Details of method of mounting insect with fine wire thermocouple inserted in thorax in such a way as to lie between muscle bands.

**Table 2. Temperature excess (° C.) in different parts of insect subjected to constant radiation of 1.5 cal./cm.²/min.**

<table>
<thead>
<tr>
<th>Position of thermocouple</th>
<th>Muscina</th>
<th>Carausius (Orthop.)</th>
<th>Schistocerca (Orthop.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Normal</td>
<td>Blackened</td>
<td>Normal</td>
</tr>
<tr>
<td>Thorax:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>On upper surface</td>
<td>—</td>
<td>7.3</td>
<td>14.2</td>
</tr>
<tr>
<td>Very close to upper surface</td>
<td>4.6</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Above centre of thorax</td>
<td>4.5</td>
<td>7.6</td>
<td>12.0</td>
</tr>
<tr>
<td>Centre</td>
<td>4.3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Below centre of thorax</td>
<td>4.1</td>
<td>(2.52)*</td>
<td>(7.65)*</td>
</tr>
<tr>
<td>Very close to lower surface</td>
<td>4.0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>On lower surface</td>
<td>4.0</td>
<td>(4.75)*</td>
<td>(11.2)*</td>
</tr>
<tr>
<td>Abdomen:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Above centre</td>
<td>6.9</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Centre</td>
<td>6.15</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Below centre</td>
<td>6.2</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

* Values arrived at by turning insect upside down.
given the temperature excess found in different parts of three insects when mounted in the air stream at a wind speed of 50 cm./sec. and radiation strength of 1.5 cal./cm.°/min. The considerable differences in temperature between the upper and lower parts of the thorax of Carausius probably result from the gut in the centre containing air. The current produced was measured on a Cambridge Instrument Co. pot galvanometer of 40 Ω resistance giving close to 1 cm. deflexion on a scale 1 m. distant for 1° C. difference of temperature between the insect and the air. The measurement of the temperature of an insect by thermocouple wires has given some difficulty in the past; Krogh (1948) showed the heat loss along thermocouple wires can be quite large. With such fine wires, however, heat transfer along the wires was found to be negligible, for neither touching the fine thermocouple wires just outside the thorax of a 3 mm. diameter insect with a hot wire, nor shielding them from the wind by means of a thin cylinder of cellophane or paper produced a difference in galvanometer reading corresponding to more than 0.05° C.

(iv) Estimation of temperature rise from rate of wing beat

The temperature rise in small insects such as Drosophila cannot readily be determined by the use of a thermocouple of this size when the insects are alive because of their small size.

![Graph](image)

Fig. 4. Variation in increase of rate of wingbeat of Drosophila with change in (a) air temperature, (b) radiation intensity.

It is possible to estimate the temperature rise of flying Drosophila when exposed to radiation by observing changes in its rate of wing beat. This has been shown to be proportional to the temperature over the normal range (Chadwick, 1939) and to decrease slowly owing to fatigue or to utilization of reserves (Williams, Barnes & Sawyer, 1943). In the present case, the rate of wing beat of a mounted and flying specimen was calibrated against air temperature by transferring it from a tube in
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a water-bath at 18°C. to tubes in water-baths at higher temperatures and back again, while the rate of wing beat was followed by an electric stroboscope. Two-minute exposures to each temperature were found to be suitable, observations of wing beat being made every 10 sec. Reference to the rate at 18°C. every 2 min. was necessary to allow correction for alteration in this basal rate due to fatigue. Immediately after calibration the same insect was transferred to the insect chamber in such a way that it was subjected to radiation from above while the rate of wing beat was followed by silhouetting it against the light of the stroboscope. This enabled the relation between wing beat and radiation to be determined. Experiments showed that light unaccompanied by appreciable heat radiation had little or no effect in raising the rate of wing beat apart from a temporary increase in the rate over 10 or 20 sec. on bringing insects from complete darkness to the light. The persistent increase of wing rate in strong radiation is therefore considered to be due solely to temperature. Comparison of the two curves, wing rate against air temperature and against radiation (Fig. 4) indicated that at a wind speed of 50 cm./sec. and radiation of 1·0 cal./cm.²/min. the temperature rise was 2·5°C. in a large wild specimen of Drosophila and 1·0–1·5°C. in a small P. melanogaster, while in the latter, at a wind speed of 10 cm./sec. (about the normal speed of flight) the temperature rise was 2·5°C.

(3) FACTORS AFFECTING TEMPERATURE EXCESS

(i) Intensity of radiation

The variation in temperature excess with radiation strength for six insects is shown in Fig. 5. In the five larger forms the conditions were: wind 50 cm./sec., temperature about 20°C., radiation 0–2·0 cal./cm.²/min. Temperature excess was measured by thermocouple. In Drosophila, run at a lower wind speed, temperature excess was assessed by change in rate of wing beat.

The relation was substantially linear in the five larger species. This linear relation is to be expected where the laws of forced convection hold good. Departures from linearity may be expected under conditions of natural convection (where temperature varies as the 0·8 power of the radiation) and where evaporation is important. The temperatures are slightly lower than would be expected at the highest radiation intensities; at these temperatures evaporation is not likely to be involved for the cuticular waxes would retain their protective function (Wigglesworth, 1945), so the discrepancy is probably due to the slight development of natural convection with the increase of buoyancy forces at higher temperatures (see § 3, (v)). In Drosophila, the relationship was not linear, but in this case radiation intensity was altered by filters, so non-linearity may have been caused by variation in absorptivity with spectral composition.

(ii) Spectral distribution of radiation

The spectral composition of the radiation was varied by inserting copper chloride and water filters between the bulb and the insect. The proportion of infra-red was varied from 8% (less than in daylight) through 40% (daylight) to 78% (greater than daylight), the total vertical radiation strength being adjusted to 0·5 cal./cm.²/min.
each time. In one case, the same radiation intensity was also provided by a domestic electric radiator giving almost entirely infra-red radiation with a peak wavelength at about 2·5μ.

Five species of flies, *Lucilia caesar* and *Phormia caerulia* with the thorax metallic green and blue, and *Eristalis tenax, E. arbustorum* and *Sphaerophoria scripta* with

![Diagram](image)

**Fig. 5.** Variation in temperature excess with total radiation intensity.

the thorax dull brown showed very little difference in temperature (under 5%) over the above range. Clearly, therefore, any differences in spectral composition in the sun’s radiation with the time of the day are of very minor importance to insects of this size.

It is probable that smaller insects may be more sensitive to spectral composition, for they no doubt transmit a larger part of the incident radiation. The absorption bands of flesh of various invertebrates was shown by Rucker (1933b) to be closely similar to those of water, and the same no doubt holds true for these forms.
Factors affecting the temperature excess of insects in sunshine

Some indication that this may be so is afforded by Drosophila, for in most of the experiments dealing with the relation of temperature (estimated by wing beat) to radiation, the latter was changed by inserting various filters so that at the highest total radiation intensity the light contained the greatest proportion of infra-red (as in the case shown in Figs. 4 and 5). In these cases the more intense radiation (richer in infra-red) produced a smaller increase in wing rate per unit radiation than did the less intense radiation. As the wing beat was more strictly proportional to radiation when the latter was altered by altering the height of the bulb, it probably indicates that a greater proportion of the infra-red than of the visible was passing through the insect.

(iii) Colour and absorptivity of insect

The colour of an object affects the proportion of radiation it absorbs, or absorptivity. Temperature excess is commonly proportional to absorptivity.

It is difficult to assess accurately the effect of the colour of an insect on its temperature by finding the temperature excess of similar insects varying in colour alone because no two insects are rarely quite alike apart from colour, and furthermore, it is not even easy to obtain temperatures which agree exactly when the same thermocouple is removed and replaced in the same insect.

Some information on the effect of colour may be gained from the experiments run for the effect of size on temperature (Fig. 7). The specimens which were of a metallic colour are marked distinctively on the graph. Their temperatures did not differ much from the average, so variation in temperature arising from colours between metallic blues and greens, dull browns and black is very slight.

This, however, gives us no idea of absorptivity, although we may expect that a dark-coloured insect is not far from being a black body. Another way of assessing the effect of colour on temperature excess is to find its temperature excess when normal and again when painted black, to convert it to a black body (absorptivity 100%) of the same size and shape. In a series of experiments, after obtaining the temperature excess of an insect as usual, the dorsal surface was painted with black oil paint or with an aqueous suspension of lamp-black and the temperature excess found again, after a suitable period to allow evaporation of the solvent. The results are given in Table 3.

The most notable point is that a number of insects were hotter (in the middle of the body) in the normal state than when painted black. As the insect absorbs the maximum amount of heat when painted black it cannot be true to say that the temperature excess varies with absorptivity. It seems better to refer to the proportion between the temperatures as apparent absorptivity. These apparent absorptivities for the normal insects ranged between 63 and 117%. Pale forms, green to dark yellow, ranged from 63 to 86%; dark forms, browns, blacks and metallic greens, blues and blacks, from 71 to 117%.

The explanation for this apparent absorptivity in excess of 100% probably lies in the site of absorption. Heat produced is carried away by conduction and convection to the air, and by conduction to the underlying body of the insect and to the other cooling surfaces (radiation being very slight). Where the surface is highly
absorbing, the heat is produced at the surface where it will readily be carried away; but where the surface absorbs little of the heat, more radiation will be available for absorption throughout the thickness of the thorax. In this case, as cooling is only at the outer surface, the inside will be hotter than the outside. Such an effect is known in other fields—for instance in the melting of snow beneath the surface at low air temperatures.

Table 3. Temperature excess (°C.) of various insects as normal and when painted, subjected to wind of 50 cm./sec. and to radiation from bulb

<table>
<thead>
<tr>
<th>Insect</th>
<th>Colour</th>
<th>Temperature excess (°C.)</th>
<th>Apparent absorptivity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carausius morosus (Orthop. Phasmidae)</td>
<td>Green*</td>
<td>7.6</td>
<td>12.0</td>
</tr>
<tr>
<td>C. morosus (Orthop. Phasmidae)</td>
<td>Green</td>
<td>1.54</td>
<td>2.20</td>
</tr>
<tr>
<td>Periplaneta americana (Orthop. Blattidae) nymph</td>
<td>Brown</td>
<td>3.23</td>
<td>4.55</td>
</tr>
<tr>
<td>Schistocerca gregaria (Orthop. Acrididae) adult</td>
<td>Dull yellow-green*</td>
<td>10.1</td>
<td>13.4</td>
</tr>
<tr>
<td>Periplaneta americana (Orthop. Blattidae) nymph</td>
<td>Brown</td>
<td>2.4</td>
<td>3.2†</td>
</tr>
<tr>
<td>Calliphora erythrocephala (Dipt. Tachinidae)</td>
<td>Dull blue-black</td>
<td>1.43</td>
<td>1.87</td>
</tr>
<tr>
<td>Vespa vulgaris (Hym. Vespidae) abdomen</td>
<td>Yellow and black</td>
<td>4.2</td>
<td>5.3†</td>
</tr>
<tr>
<td>Schistocerca gregaria (Orthop. Acrididae) stage V hopper</td>
<td>Dull yellow-green</td>
<td>2.0</td>
<td>2.5†</td>
</tr>
<tr>
<td>S. gregaria (Orthop. Acrididae) stage V hopper</td>
<td>Dark yellow</td>
<td>1.76</td>
<td>2.2</td>
</tr>
<tr>
<td>S. gregaria (Orthop. Acrididae) stage IV hopper</td>
<td>Dark yellow</td>
<td>2.90</td>
<td>3.36</td>
</tr>
<tr>
<td>Lucilia caesar (Dipt. Tachinidae)</td>
<td>Metallic green</td>
<td>2.4</td>
<td>2.4†</td>
</tr>
<tr>
<td>Phormia caerulia (Dipt. Tachinidae)</td>
<td>Metallic blue-black*</td>
<td>8.2</td>
<td>7.9</td>
</tr>
<tr>
<td>Phormia caerulia (Dipt. Tachinidae)</td>
<td>Metallic blue-black*</td>
<td>3.0</td>
<td>2.8†</td>
</tr>
<tr>
<td>Erinolophia tenax (Dipt. Syrphidae)</td>
<td>Brown</td>
<td>3.5</td>
<td>3.2†</td>
</tr>
<tr>
<td>Sarcophaga carnaria (Dipt. Tachinidae)</td>
<td>Dull blue-black</td>
<td>2.8</td>
<td>2.5†</td>
</tr>
<tr>
<td>Mesembrina meridiana (Dipt. Tachinidae)</td>
<td>Black</td>
<td>3.5</td>
<td>3.0†</td>
</tr>
</tbody>
</table>

* Experiments run at 1.5 cal./cm.²/min. with water filter; otherwise run at 0.5 cal. with copper chloride filter to give correct spectral composition.
† Specimens painted with aqueous suspension of lamp-black; otherwise artists’ oil paints used.

That the painting of an insect affects the distribution of temperature is shown in Table 2 for the stick insect and the locust. The normal stick insect was a little cooler on the upper surface than a little way inside the thorax; in the normal locust the temperatures were equal. Blackening caused a great increase in the surface temperature and in this case a much smaller increase in the internal temperatures. It is,
moreover, interesting to note that the lower surface of Carausius, both normal and when blackened, intercepted enough of the radiation which had passed through the thickness of the body to make the ventral surface hotter than the inside.

The range of effect to be expected in colour alone was investigated by painting some of the specimens green or white. For although the pigments in paint are not those found in the insect, the range of temperatures of normal insects of various colours should be fairly similar to that of a series of painted insects, in so far that differences of temperature are due to differences in colour in the visible alone. The apparent absorptivities of green-painted specimens lay between 88 and 97%, of white, 64 and 85%. This high absorptivity of the light-green or white-painted insect arises from the fact that, as Gunn (1942) has pointed out, a large part of the radiation is in the infra-red, of which the white paint (titanium white) absorbs a large part. As half the radiation is in the infra-red, temperature bears as much relation to absorption in the infra-red as to absorption in the visible.

It may be noted that roughly similar results were obtained by Dorno (1931) (quoted by Geiger, 1950) for painted wooden posts heated by sunshine. The temperature of a white-painted post reached 64% of that of a black post. These experiments have given results which are in reasonable agreement with the absorptivity measurements of Rucker (1933a, b, 1934) and Duspiva & Cerny (1934). From their measurements, if we say that in extreme cases insects which differ only in colour will have a constant absorption of say 50% in the infra-red and an absorption in the visible which varies from 26 to 95%, then the lightest insect, a chalky white form, will be expected to achieve 52% of the temperature excess of the darkest; insects of the more usual light colours (that is, blues, greens, yellows) will be expected to achieve 75% of the temperature excess of the dark forms. It is, however, noticeable that in many light-coloured insects the thorax itself is dark. Temperature differences due to variation in colour will therefore be of minor importance.

It is convenient to consider pubescence at this point. In the experiments run for the effect of size on temperature (Fig. 7), pubescent specimens appear to be no warmer than their non-pubescent neighbours. This is perhaps surprising, but as the experiments were run at a wind speed of 50 cm./sec., quite possibly the effects of pubescence are only of significance at lower wind speeds where viscous forces in the air flow come more into play.

(iv) Size

The curves of the increase of temperature against time obtained for six insects at a wind speed of 50 cm./sec., when a radiation strength of 1.5 cal./cm.²/min. was switched on, are shown in Fig. 6. The larger insects attained the higher temperatures and took longer to attain them.

The relation of equilibrium temperature excess to size for insects (Table 4) and for spheres of black plasticine at the same radiation and wind speed is shown in Fig. 7 as a log-log plot. The size measured was the diameter in the case of the plasticine spheres and the maximum breadth of the thorax close to the base of the wings in the case of the insects. In the plasticine spheres the temperature excess varied as a power of the size between 0.7 for spheres below 0.3 cm., and 0.4 for
larger sizes (0.3–2.0 cm.). Size for size, temperatures of the locusts varied between the temperature of the spheres and twice this value. Most of the points for these insects are ranged about a line indicating that temperature excess varies as about the 0.4 power of the size. Temperatures of the Diptera and Hymenoptera were from half as much again to three times as great as those of the spheres, varying approximately as the 1.0 power of the size.

![Graph showing temperature excess in various insects](image)

**Fig. 6.** Increase in temperature excess in various insects when radiation of 1.5 cal./cm.⁴/min. switched on. Wind 50 cm./sec. In *Bombus* departures from smooth curve coincide with slight movements of thorax, wings and legs.

Temperature may be expected to vary with the 0.5 to 0.6 power of the size when conditions of forced convection prevail, but when velocity or size becomes very small this power may be expected to increase to 1.0. The plasticine spheres agree reasonably well with theory, but the insects, particularly the Diptera and Hymenoptera, show a much steeper slope than is expected. Why is the slope so steep? Transition to the 1.0 power of the size should only occur in much smaller specimens (i.e. when *Nu* approaches 2, see Appendix.) The possibility of part of the effect being the loss of
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heat via the thermocouple wires in the smallest forms of about 0.3 cm. diameter cannot be entirely ruled out. Natural convection effects cannot be the cause because a tendency to natural convection only results in a reduction of temperature of the very largest specimens at this wind speed; and this would cause the curve to be less steep; to tend towards the 0.2 power. The most likely explanation is that the steepness is due to change in absorptivity or the position of absorption (perhaps both) with size.

Table 4. Relation of temperature excess to size in a series of insects of squat body form (Diptera-Hymenoptera type) and of elongate body form (locust type), at a radiation strength of 1.5 cal./cm.²/min. and a wind speed of 50 cm./sec.

<table>
<thead>
<tr>
<th>Breadth of thorax (cm.)</th>
<th>Diptera-Hymenoptera type, species</th>
<th>Mean temp. (°C)</th>
<th>Locust type, species</th>
<th>Mean temp. (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.5-2.5</td>
<td>Sinaphyris scripta (Dipt. Syrphidae), 3, 1</td>
<td>5.2</td>
<td>Schistocerca gregaria (Orthop. Acrididae), stage I hopper, 2</td>
<td>4.5</td>
</tr>
<tr>
<td></td>
<td>Syrta pipiens (Dipt. Syrphidae), 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Musca domestica (Dipt. Anthomyiidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Eristalis arbutorum (Dipt. Syrphidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.6-3.5</td>
<td>Lucilia caesar (Dipt. Tachinidae), 2</td>
<td>8.9</td>
<td>Carausius morosus (Orthop. Phasmidae)</td>
<td>6.7</td>
</tr>
<tr>
<td></td>
<td>Sarcophaga carnaria (Dipt. Tachinidae), 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Phormia caerulea (Dipt. Tachinidae), 3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Eristalis arbutorum (Dipt. Syrphidae)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Apis mellifera (Hym. Apidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Vespa vulgaris (Hym. Vespidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.6-4.5</td>
<td>Calliphora erythrocephala (Dipt. Tachinidae), 2</td>
<td>9.6</td>
<td>Carausius morosus (Orthop. Phasmidae)</td>
<td>6.2</td>
</tr>
<tr>
<td></td>
<td>Echinomyia fera (Dipt. Tachinidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Apis mellifera (Hym. Apidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Psithyrus campestris (Hym. Bombidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Eristalis nemorum (Dipt. Syrphidae)</td>
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<td></td>
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<tr>
<td></td>
<td>Mesembrina meridiana (Dipt. Tachinidae)</td>
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<td></td>
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<tr>
<td></td>
<td>Eristalis tenax (Dipt. Syrphidae), 3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bombus territ,us w. (Hym. Bombidae)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.6-6.5</td>
<td>Psithyrus campestris (Hym. Bombidae)</td>
<td>8.0</td>
<td>S. gregaria (Orthop. Acrididae), stage IV hopper, 3</td>
<td>7.9</td>
</tr>
<tr>
<td>6.6-8.5</td>
<td>Bombus lapidarius w. (Hym. Bombidae)</td>
<td>12.0</td>
<td>S. gregaria (Orthop. Acrididae), stage V hopper, 4</td>
<td>6.4</td>
</tr>
<tr>
<td>8.6-10.5</td>
<td></td>
<td>9.6</td>
<td>S. gregaria (Orthop. Acrididae), adult, 2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Periplaneta americana (Orthop. Blatidae), nymph, 2</td>
<td></td>
</tr>
</tbody>
</table>

(v) Wind

Curves relating temperature excess to wind speed at a radiation strength of 1.5 cal./cm.²/min. are given for two plasticine spheres and for a number of insects of varying size as a log-log plot in Fig. 8. In both insects and spheres temperature varied inversely as the square root of the wind velocity when the latter was above 20–30 cm./sec., but below these wind speeds the slope decreased towards the point (not reached) where temperature would be independent of wind velocity. This
indicates that above 20–30 cm./sec., forced convection was occurring, but below these speeds conditions of natural convection with temperature independent of wind speed were approached. Larger specimens showed an approach to natural convection at a higher wind speed than did smaller specimens because of their greater temperatures.

Fig. 7. Variation in temperature excess with size for a series of insects and plasticine spheres, log-log plot. The slope of the curves changes with size, the temperature excess varying with a power of the size between 1.0 and 0.37. Radiation 1.5 cal./cm.²/min., wind 50 cm./sec.

There is a certain amount of variation in temperature according to the orientation of the insect. The above experiments were all performed with the thermocouple in the thorax and the insect facing into the wind. Variation in temperature excess according to orientation to wind (orientation to radiation being constant) is shown for five insects in Table 5. There was practically no difference in *Periplaneta*, a *squat form*, but in *Carausius*, of elongate cylindrical shape, the temperature was reduced by nearly one half by turning sideways on. Thus an elongate insect may well exercise some control of its body temperature by orientation to wind. This is to be expected, for it is known that heat loss from a cylinder with air flow normal to the long axis is about twice that with the air flow in the direction of the long axis.
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Fig. 8. Variation in temperature excess with wind velocity, log-log plot. Each line represents a run for a single insect or plasticine sphere. The slope of the curves changes with wind velocity, temperature excess varying inversely with the square root of the wind speed at high speeds, but tending to be independent of wind at low speeds (transition between natural and forced convection). Radiation 1.5 cal./cm.²/min., wind 5–150 cm./sec.

Table 5. Variation in temperature excess with orientation to wind for insects of differing shape

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion length/breadth of insect</th>
<th>Temp. facing air stream (as usual)</th>
<th>Temp. excess at 45° to wind, as percentage of temp. excess facing wind (%)</th>
<th>Temp. excess at 90° to wind, as percentage of temp. excess facing wind (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periplaneta americana (Orthop. Blattidae), nymph</td>
<td>2.5 : 1</td>
<td>3.16</td>
<td>99</td>
<td>99</td>
</tr>
<tr>
<td>Calliphora erythrocephala (Dipt. Tachinidae)</td>
<td>2.6 : 1</td>
<td>1.54</td>
<td>100</td>
<td>97</td>
</tr>
<tr>
<td>Schistocerca gregaria (Orthop. Acrididae), stage IV hopper</td>
<td>5.6 : 1</td>
<td>2.99</td>
<td>98</td>
<td>88</td>
</tr>
<tr>
<td>Schistocerca gregaria (Orthop. Acrididae), stage V hopper</td>
<td>5.4 : 1</td>
<td>1.76</td>
<td>—</td>
<td>86</td>
</tr>
<tr>
<td>Carausius morosus (Orthop. Phasmidae)</td>
<td>15.1 : 1</td>
<td>1.58</td>
<td>67</td>
<td>56</td>
</tr>
</tbody>
</table>
(vi) Evaporation and metabolism

Specimens of Calliphora, Phormia, Muscina and Schistocerca when mounted and subjected to wind speeds of 10-100 cm./sec. and no radiation approximated to the temperature of the air stream to 0·05° C. or closer, the temperature drop from evaporation being practically negligible. This is to be expected, as the water loss is slight.

It is well known that the metabolic activity of flight results in a substantial rise in temperature in large insects. A similar smaller rise occurs in these smaller forms. When a live fly was mounted with a thermocouple in the thorax, flight quite often appeared to be normal in the rate of wing beat and duration; when flying began in a mounted specimen of Calliphora with no radiation and a wind speed of 50 cm./sec. the temperature typically showed a momentary drop of about 0·1° C., then a rise of up to 2·0° C. in 1 or 2 min. Most of the rise occurred in the first 30 sec., and it was followed by a slow drop of 1·0° C. after flight had continued for some minutes. This temperature rise from the metabolic activity of flight was found to be dependent upon wind speed as was the temperature rise from radiation; thus with Muscina flying at wind speeds of 0, 50 and 100 cm./sec., with no radiation, the temperatures attained were 1·3, 1·1 and 0·8° C. above that of the air, respectively. Occasionally the temperature of a mounted but apparently inactive insect could be seen to rise; in the case of Calliphora, to 0·75° C. above that of the air (with wind at 50 cm./sec. and no radiation); the same phenomenon was observed by Krogh & Zeuthen (1941) in various larger insects. Sometimes this led to flight, but sometimes the temperature dropped again to that of the air. With this form of activity, the temperature never rose to more than 0·8° C. above that of the air, as against some 1·5° C. for full flight under the same conditions. This warming was not preceded by the momentary drop in temperature that marked the initiation of flight. The momentary drop is probably due to internal ventilation and evaporation.

This metabolic heating might be expected to result in an insect becoming hotter when flying in sunshine than when basking, other things being equal. But such is not the case. When flight began during exposure to radiation of 1·5 cal./cm.²/min. the temperatures of Calliphora and Muscina which had become steady at 4–6° C. above that of the air, showed only a slight change. This ranged between a decrease of 0·5° C. and an increase of 0·3° C., notwithstanding the fact that in the absence of radiation flight would cause a rise of 1·5–2·5° C. This indicates that the extra heat input was counterbalanced by the extra loss from internal ventilation and evaporation. It follows that similar temperatures attained by flight activity and by radiation do not represent similar rates of heat in-put.

The heating effect of metabolism becomes less important compared with that of the sun as size decreases. Thus while an insect the size of a hawk moth would appear to attain a roughly similar temperature excess by metabolism as it would in strong sunshine, a small fly (Muscina) will only attain by metabolism about a fifth of its own sunshine temperature excess. Metabolic heating will decrease with the cube of the linear dimension, radiative heating with the square.
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DISCUSSION

The position of long-wave radiation has been neglected so far. An insect is probably usually cooler than its surroundings, for in both natural and forced convection the rate of heat loss is greater from a small isolated body than from a flat surface. An insect will therefore gain heat by radiation from the background and this gain will be greatest with a dry background, for moist vegetation is kept cool by evaporation. As a probably exceptional case, an insect at 20° C. surrounded by a hemispherical background at 40° C. can be shown to gain heat at about 0.1 cal./cm.²/min. Such a temperature difference of 20° C. would only be maintained in bright sunshine with direct plus reflected short-wave radiation of at least 1.5 cal./cm.²/min. Over the small range of temperature considered, radiation is nearly proportional to temperature difference, and a more likely temperature difference of 10° C. would result in a long-wave radiation contribution of only some 4% of the total.

The main factors controlling the temperature excess for small insects are radiation, wind and size. For insects of the Diptera-Hymenoptera type resting in a position where they were subjected to a 50 cm./sec. wind and strong sunshine from above, the temperature excess would be: Drosophila (1.5 mm. broad), 1.5° C.; Syritta pipiens (2 mm. broad), 5° C.; Calliphora (4 mm. broad), 8° C.; Bombus (8 mm. broad), 12° C. Insects similar to the locust would be half to two-thirds as hot, size for size. These figures hold for bright sunshine in spring (1.5 cal./cm.²/min.). Later in the year the sunshine is commonly weaker (1.0 cal./cm.²/min.) and the temperature will be two-thirds of the above. A reasonable value for sunshine just visible through cloud is 0.25 cal./cm.²/min.; in this case the temperature will be one-sixth that of the above. If the wind dropped from 50 to 10 cm./sec. the temperature would be doubled in the case of the smaller insects but would only be half as much again in the larger forms. Still lower winds result in still higher temperatures—possibly half as much again as the 10 cm./sec. values; we do not know the limit for the maximum temperatures attainable under true natural convection. A very small alteration in microclimatic temperature at these low speeds can cause great differences in temperature. A limited amount of temperature control is possible by orientation to wind, but this method is only open to insects of the locust type. Colour has little effect, not more than some 25% as a rule; most insects, however, have a dark thorax.

Calculation of the temperature of insects from the relations which are known to exist between temperature excess, size and wind speed suffer from the disadvantage that the convection conditions which prevail close to the ground lie between those of natural and forced convection, where the expressions appropriate to either do not hold good. This region could, however, be covered by empirical relations obtained by the manner employed in this paper. The application of such observations to the field is at present limited by the lack of field observations on microclimate, particularly wind speed and temperature close to the ground.

It seems probable that to attain as high a temperature excess as possible for a given size is of selective significance, for insects are so dependent on temperature for their activity. This suggestion is supported by the way in which the thorax of an
insect would appear to be adapted to that end. The thorax of an insect may be regarded as a sphere protected from convective heat loss by the head in front and the abdomen behind. The heat loss from a sphere is greatest on the sides towards and away from the air flow and least at the sides (see Bairstow, 1939). The Diptera and Hymenoptera, which on morphological grounds include the most highly developed forms, show a much greater temperature excess than the locust, size for size, and in these the head and abdomen would appear to be attached to the thorax by as slender supports as possible, thus minimizing conduction. The layer of air between the head and thorax, and thorax and abdomen is probably kept stagnant by pubescence; conductivity through such a layer of air is very small. The colour of the thorax is usually dark, and sometimes the structure is such that the apparent absorptivity can be in excess of 100%. The outer surfaces of the thorax are frequently covered with bristles or pubescence, which although it does not apparently increase the temperature excess in the small range of forms studied at a wind speed of 50 cm./sec., it may well be that it has an important effect at very low speeds where viscous forces in the air stream come more into play. This is highly suggestive that the body form of the most highly developed types has evolved in response to the necessity for obtaining the maximum warmth from the sun.

**SUMMARY**

1. The temperature excess developed by insects under known radiation strength equivalent to sunshine has been studied in relation to modifying factors in a wind tunnel in the laboratory.

2. Temperature excess was measured by a thermocouple unit in the larger insects, and by the increase in rate of wing beat in *Drosophila*.

3. Temperature excess varied directly with radiation strength.

4. For insects of breadth greater than 0.3 cm. spectral composition of radiation over the normal sunshine range was of negligible importance to the temperature excess.

5. The effect of colour on the temperature excess was slight. Absorptivity was estimated by comparing temperatures of normal and black-painted insects. Some insects were hotter in the normal state because of change in the site of absorption of heat. White-painted insects were 64–85% as hot as when black painted, because the white paint still absorbs infra-red radiation.

6. Temperature excess varied with a power of the size between 0.7 and 0.4 in the plasticine spheres, according to size. Temperature excess of the locust type varied as about the 0.4 power of the size; of the Diptera-Hymenoptera type, as about the 1.0 power. Size for size, compared with the spheres, the locust became between half as hot again and twice as hot, and the Diptera-Hymenoptera type between half as hot again and three times as hot, as the plasticine spheres.

7. Temperature excess varied inversely as the square root of the wind speed above speeds of 20–30 cm./sec. and tended to become independent at lower speeds, with the transition between forced and natural convection. The latter condition will be more important close to the ground.
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8. Temperature rise by flight activity is not additive to temperature rise from radiation because it is associated with extra cooling.

9. Evolution of insects from the type of the Orthoptera to the Diptera and Hymenoptera has been associated with the attainment of greater temperature excess for given body size. This is probably of selective significance.

This work was carried out at the Department of Zoology and Comparative Anatomy at Oxford, supported by an Agricultural Research Council grant, and in the Department of Biology, St Thomas’s Hospital Medical School, London. The wind tunnel used was originally constructed at the School of Agriculture, Cambridge. For facilities and encouragement I am grateful to Prof. A. C. Hardy, F.R.S., Dr A. G. Hamilton, Mr F. R. Petherbridge, Mr J. H. Stapley and Mr D. W. Wright. I am indebted to Dr G. D. Robinson for the loan of a Michelson actinometer and to Dr W. Cockrane and Dr M. Fishenden for helpful discussion. I am grateful to Prof. A. C. Hardy, F.R.S., for reading the manuscript and to my wife for her help at many stages.

APPENDIX

The relationships for the convective heat loss from cylinders and spheres, as given by Fishenden & Saunders (1950) are:

(i) In the absence of applied air flow (natural convection—here considered in the streamline range), for cylinders,

$$\frac{H}{\theta} = 0.24 \left(\frac{\theta}{d}\right)^{0.35},$$

where $H$ = heat transfer per unit area, unit time; $\theta$ = temperature excess at surface; $d$ = diameter. No data is available for spheres.

(ii) In the presence of an applied air flow (forced convection), with air moving across a cylinder, for Reynolds number ($Re$) 1000–100,000

$$Nu = 0.24 \, Re^{0.4},$$

where $Nu$ = Nusselt number, $Hd/k\theta$; $Re = vpl/\mu$; $v$ = velocity of air; $k$ = conductivity of the air; $\rho$ = density of the air; $\mu$ = viscosity of the air.

In the range $Re = 10–200$ covered in this paper, the relation $Nu = 0.7 \, Re^{0.4}$ might be expected to be more appropriate.

With air moving along a cylinder, which is more comparable to the case of an insect facing the air stream, heat flow is half this value. For a sphere the formula is the same apart from the constant. When $v$ is small, $Nu$ reaches a limiting value of 2; hence,

$$\frac{H}{\theta} = \frac{2k}{d}.$$

Now the factor in which we are most interested is the temperature excess of the inside of the thorax. In engineering problems the factor which is of prime importance is the heat transfer coefficient, $H/\theta$. In these experiments, as the heat has been applied by radiation and we do not know the true absorptivity, we do not know the
rate of heat gain, $H$. Neither do we know the true mean surface temperature excess, $(\theta)$ although it is probable that it is not very different from the temperature of the inside of the thorax. We are therefore not in a position to calculate exactly either the heat transfer coefficient or the Nusselt number. It is therefore most suitable to consider simply the temperature excess in relation to the other terms, i.e. radiation, size and wind speed, etc.

REFERENCES


