FACTORS DETERMINING THE TEMPERATURE OF TERRESTRIAL ARTHROPODS IN SUNLIGHT

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(With Eight Text-figures)

INTRODUCTION

It has long been realized that the so-called cold-blooded animals are not always cold: in the sun their temperature may rise considerably above that of the surrounding air and even surpass that to which the homoiotherms are regulated. Some measurements have been made of such temperatures (Gunn, 1942), but the experimental difficulties are considerable and can hardly be faced with anything under the size of a large insect. There is, however, another approach to the subject. The temperature of any body in equilibrium with its surroundings, whether animate or inanimate, is that at which the algebraical sum of the heat exchanges across its surface is zero. Furthermore, it will be shown in the third part of this paper that the metabolic heat production of an arthropod on the ground is insignificant compared with the heat received from the sun; and similarly, the amount of this heat lost by evaporation is normally insignificant compared with that lost by radiation and convection. Therefore the temperature of such an animal, like that of an inanimate body, is determined by the balance of radiative, convective, and perhaps conductive, heat exchanges. The factors which influence this balance may be studied with the help of models in a way which would be difficult or impossible with living animals, and by introducing into the model some simplification of shape and colour it is possible to compare the equilibrium temperatures actually recorded with those which would be expected from theoretical considerations.

It must be emphasized that this paper is concerned with the equilibrium temperature of bodies in direct sunlight. Such an inquiry has a direct application to those animals, notably grasshoppers and locusts, certain beetles and many arachnids, which habitually expose themselves to the sun. It also has a more general significance inasmuch as the danger of overheating, together with that of desiccation, has most likely played an important part in the evolution of terrestrial arthropods.

FIELD MEASUREMENTS OF EQUILIBRIUM TEMPERATURES

Preliminary measurements

These were made on blackened brass spheres, diameters 1/4, 1/2 and 3/4 in., mounted on Perspex (i.e. low conductivity) feet with the lower surface of the sphere 1/16 diameters from the 'ground' (a tufnol sheet flush with rough bare earth). The temperature of
each sphere was measured with a thermocouple made of 0.0048 in. diameter nichrome and constantan wire in which thermal losses were insignificant. The measurements established the following points:

(a) The temperature of the spheres rose to 40–45°C on a clear day in June.

(b) There was a significant difference in equilibrium temperature between the small and medium spheres under the same conditions.

(c) Slight changes in height above ground had a considerable effect on equilibrium temperature.

(d) The steep gradient of air temperature within an inch of the ground made it impossible to express measurements as differences in temperature between the body and the immediately surrounding air.

Effect on temperature of height above the ground

(i) Methods. To study the effect of changes of height on the temperature of a body it is necessary to make a series of measurements over a period of time during which changes in the sky or the mean wind may occur. Such changes may be at least partially allowed for by expressing the temperatures of the ‘experimental’ body as differences from those of a ‘reference’ body similarly exposed in a fixed position. Also for observation close to the ground it is desirable to use a body whose vertical dimension is as small as possible. For these reasons two similar brass disks were used, $\frac{3}{8}$ in. diameter $\times \frac{3}{4}$ in. thick, painted matt black and fitted with type U 2361/20 thermistors (Standard Telephones and Cables Ltd.) connected to a stabilized voltage of about 4 V. Details of a disk, thermistor assembly and the electrical circuit are shown in Fig. 1. The ammeters could either be read directly, or their readings could be recorded by casting a shadow of the needles on a slit beneath which a drum of light-sensitive paper revolved, the light being interrupted at intervals to provide time marks. For calibration the disks were lowered into test-tubes, each containing a thermometer, plugged with cotton-wool and fixed into a large vacuum flask containing a cooling coil. The flask was initially filled with warm water which was cooled a few degrees between each set of readings. A sensitivity of approximately 1 mm./°C was obtained. The stability of the circuits and the zero settings were checked from time to time by replacing the thermistors by fixed vitreous resistors. It can be shown that neither the heat conducted down the 0.002 in. diameter platinum leads nor the heat generated by the very small current in the thermistors could have a significant effect upon the temperature of the disks.

All the following measurements were made on a sheltered lawn at the Entomological Field Station, Cambridge, during the summer of 1950.

(ii) Equilibrium temperatures in free air. At about 2 ft. above the ground the change in temperature with height is very small—less than 1°C between 18 and 30 in. It is convenient to refer to the disk temperature at such heights as that in ‘free air’. Table 1 shows the results of a series of measurements on a disk 30 in. above the lawn on four separate occasions, the temperature given in each case being the mean
Temperature of terrestrial arthropods in sunlight

difference between disk temperature and shade (screen) temperature, the former of course always being the hotter.

(iii) Equilibrium temperature close to the ground. Not only does the disk temperature rise close to the ground but it becomes closely dependent upon the exact height above the surface. A \( 1 \times 1 \) in. clearing was plucked in the lawn, and measurements were made with the disk just touching the soil, and at various heights up to 1 in. which was approximately the height of the grass. Simultaneous measurements were made of an exactly similar disk 30 in. above the lawn nearby and the results are expressed

![Diagram](image)

**Table 1. Equilibrium temperature of disk 30 in. from ground**

<table>
<thead>
<tr>
<th>Date (1950)</th>
<th>Time (G.M.T.) and sun's altitude</th>
<th>No. of readings</th>
<th>Air temp. (°C.)</th>
<th>Mean temp. diff. and S.D. (°C.)</th>
<th>Cloud</th>
</tr>
</thead>
<tbody>
<tr>
<td>29 June</td>
<td>09.00-10.30 45-56° alt.</td>
<td>13</td>
<td>24.5</td>
<td>9.0 ± 1.5</td>
<td>Nil</td>
</tr>
<tr>
<td>30 June</td>
<td>10.00-15.00 54-61° alt.</td>
<td>33</td>
<td>20.5</td>
<td>12.4 ± 1.8</td>
<td>6/10 cumulus</td>
</tr>
<tr>
<td>7 July</td>
<td>14.00-16.00 53-56° alt.</td>
<td>20</td>
<td>21.0</td>
<td>9.0 ± 0.9</td>
<td>Hazy, some cumulus</td>
</tr>
<tr>
<td>19 Sept.</td>
<td>10.30-12.00 36-39° alt.</td>
<td>22</td>
<td>14.5</td>
<td>20.2 ± 2.8</td>
<td>6/10 cumulus</td>
</tr>
</tbody>
</table>
(Table 2 and Fig. 2a) as differences in temperature between the two, the disk close to the ground always being the hotter.

These measurements (which are typical of several series) show that the disk level

![Graph](image-url)

Fig. 2. Variation of equilibrium temperature of a ½ in. disk with height above ground: (a) on a lawn (height of grass c. 1 in.); (b) on an 'artificial lawn' of 2 in. drinking straws on a metal base at two different temperatures of the base.

### Table 2. Effect of height close to the ground on equilibrium temperature

(29 June 1950, 13.30-14.30 G.M.T., 57-53° altitude, screen temperature 27° C., cloud nil.)

<table>
<thead>
<tr>
<th>Height above soil (in.)</th>
<th>No. of readings</th>
<th>Mean temp. difference (°C.)</th>
<th>Mean temp. reference disk (°C.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>6</td>
<td>16.6 ± 1.7</td>
<td>36.9 ± 1.9</td>
</tr>
<tr>
<td>1</td>
<td>3</td>
<td>15.7 ± 0.1</td>
<td>38.1 ± 0.4</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>12.5 ± 0.8</td>
<td>38.0 ± 0.3</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>8.5 ± 0.6</td>
<td>39.4 ± 0.6</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>4.1 ± 0.5</td>
<td>39.3 ± 0.1</td>
</tr>
</tbody>
</table>

with the tips of the grass is about 5° C. hotter than the similar disk in free air (30 in.); and that within the grass itself there is a very steep gradient so that the disk touching or almost touching the ground is about 15° C. hotter than the disk in free air. As the latter may be 10° C. or more hotter than the shade temperature, the
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A disk almost touching the ground may be 50° C. Actually the highest temperature recorded was 55° C.

(iv) Effect of ground temperature. Air temperature increases with decreasing height above a warm surface, and this may be expected to cause the rise in equilibrium temperature of the disk shown in Fig. 2a. But wind velocity falls with decreasing height, and to estimate the relative effect of the two factors an ‘artificial lawn’ was constructed, the ‘ground’ temperature of which could be both measured and controlled. The ‘lawn’ was made of drinking straws 2 in. high spaced randomly about 1 in. apart on a galvanized iron sheet 18 × 18 in., beneath which was a cooling coil (see Fig. 3). The variation of disk temperature with height was found: first, when the ‘ground’ was uncooled; and secondly, when it was lowered 18° C. Results are shown in Table 3 and Fig. 2b. As usual, the temperature of the experimental disk is expressed in terms of the difference from a similar (cooler) disk at a height of 30 in. nearby. The results show the overriding effect of surface temperature upon changes in disk temperature with height: when the ground is cooled the air close to it is also cooled, while that higher up is warmed by the sun-warmed ‘vegetation’; and the disk temperature reflects this profile. It is interesting to note the similarity between this profile and that of air temperature among natural...

![Diagram of artificial lawn](image)

Figure 3. Details of ‘artificial lawn’.

Table 3. Effect of ground temperature on disk temperature

(4 Aug. 1950, 12.00–14.00 G.M.T., 54°–48° altitude, screen temperature 22° C., cloud 3/10 cumulus.)

<table>
<thead>
<tr>
<th>Height above ‘ground’ (in.)</th>
<th>Mean ground temperature 53° C.</th>
<th>Mean ground temperature 35° C.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Temp. difference (° C.)</td>
<td>Ref. disk temp. (° C.)</td>
</tr>
<tr>
<td>Just clear</td>
<td>21.2</td>
<td>32.6</td>
</tr>
<tr>
<td>¼</td>
<td>19.9</td>
<td>31.9</td>
</tr>
<tr>
<td>½</td>
<td>18.3</td>
<td>31.5</td>
</tr>
<tr>
<td>1</td>
<td>18.5</td>
<td>36.9</td>
</tr>
<tr>
<td>1½</td>
<td>15.6</td>
<td>33.2</td>
</tr>
<tr>
<td>2</td>
<td>9.7</td>
<td>33.6</td>
</tr>
</tbody>
</table>

Table 3. Effect of ground temperature on disk temperature
vegetation (Geiger, 1950, p. 282), where a similar effect is produced by the vegetation intercepting the solar radiation and so leaving the underlying ground relatively cool.

**Effect of absolute size on equilibrium temperature**

It will be shown later that there are good reasons for expecting that the equilibrium temperature of similar bodies will depend on their absolute size. That this is the case was shown by measuring the temperature in free air of three matt black disks \( \frac{2}{3} \times \frac{1}{1} \text{ in.}, \frac{2}{3} \times \frac{2}{1} \text{ in.}, \text{ and } \frac{2}{3} \times \frac{3}{1} \text{ in.} \). Temperatures were measured with 0.0016 in. nichrome-constantan thermocouples embedded in soft solder in a groove cut along a diameter of the disks. At about 15 cm. from the disk the leads were brazed to thicker wires of the same alloys and the circuit was completed through a galvanometer and melting-ice cold junction. The disks were calibrated in a thermostatically controlled water-bath whose temperature was changed in steps of about 5° C. over the required range. A sensitivity of about 1.5° C./mm. was obtained.

Table 4. **Difference of temperature between similar disks of different size**

(19 Sept. 1950, 10.30–12.00 G.M.T., 36–39° altitude, screen temperature 14.5° C., cloud 7/10 cumulus.)

<table>
<thead>
<tr>
<th>Temp. group (°C.)</th>
<th>No. of observations</th>
<th>( \frac{2}{3} \text{ in. disk} )</th>
<th>( \frac{1}{1} \text{ in. disk} )</th>
<th>( \frac{2}{3} \text{ in. disk} )</th>
<th>( \frac{2}{3} \text{ in. disk} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>29</td>
<td>1</td>
<td>28.9</td>
<td>25.2</td>
<td>23.8</td>
<td>5.1</td>
</tr>
<tr>
<td>31</td>
<td>3</td>
<td>31.2</td>
<td>27.2</td>
<td>25.9</td>
<td>5.3</td>
</tr>
<tr>
<td>33</td>
<td>4</td>
<td>32.6</td>
<td>27.9</td>
<td>26.0</td>
<td>6.6</td>
</tr>
<tr>
<td>35</td>
<td>7</td>
<td>34.8</td>
<td>29.4</td>
<td>27.3</td>
<td>7.5</td>
</tr>
<tr>
<td>37</td>
<td>1</td>
<td>36.9</td>
<td>31.2</td>
<td>29.5</td>
<td>7.4</td>
</tr>
<tr>
<td>39</td>
<td>5</td>
<td>38.4</td>
<td>32.3</td>
<td>29.5</td>
<td>8.9</td>
</tr>
<tr>
<td>Mean</td>
<td>21</td>
<td>34.2</td>
<td>29.5</td>
<td>27.3</td>
<td>6.9</td>
</tr>
</tbody>
</table>

\( t = \) difference in mean temperature from that of the \( \frac{2}{3} \text{ in. disk} \).

The results consist of about twenty almost simultaneous observations of the temperature of the three disks. The temperatures of the \( \frac{2}{3} \text{ in. disk} \) have been arranged in two-degree groups and the means of these temperatures have been calculated together with the corresponding means for the \( \frac{1}{1} \text{ and } \frac{2}{3} \text{ in. disk} \). These figures are given in Table 4, and they show that the temperature of the disks does decrease with size so that when the temperature of the \( \frac{2}{3} \text{ in. disk} \) ranges between 29 and 39° C., the \( \frac{1}{1} \text{ in. disk} \) is 3.7–6.1° C. cooler and the \( \frac{2}{3} \text{ in. disk} \) is 5.1–8.9° C. cooler. Fig. 4 shows the dependence upon size of the mean temperatures of all the observations on each disk.

**Correlation between temperatures of a disk and an insect**

Owing to the persistent bad weather during the summer when this work was done very few measurements of living animals were made, nor did an opportunity arise of comparing the temperature of an animal with that of a similarly shaped and coloured model. Comparisons between the temperature of the \( \frac{2}{3} \times \frac{1}{1} \text{ in. matt black} \)
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Fig. 4. Effect of size on the equilibrium temperature of a disk in free air.

A THEORETICAL TREATMENT OF THE TEMPERATURE EQUILIBRIUM OF SMALL ANIMALS IN SUNLIGHT

The factors involved in the heat exchange

(i) The condition of equilibrium. Any body is in temperature equilibrium with its surroundings when the net heat exchange across its surface is zero. This therefore is the condition which determines the equilibrium temperature (henceforth called the 'temperature', equilibrium conditions being assumed) of an animal. The types of heat exchange are: net radiation, convection, conduction, metabolism, evaporation.
(ii) **Radiation.** The net radiation load is made up of both solar and long-wave radiation. **Solar radiation** (0.3–2.0 μ in wave-length with about half the energy in the infra-red) is received directly, diffusely by the sky, and by reflexion from the ground. **Long-wave radiation** (a broad band with a maximum at about 10 μ), which all matter produces by virtue of its absolute temperature (5.7 x 10⁻⁹ mW./cm.² and degrees absolute), is both lost by the body and also gained from the surrounding ground and the water vapour and carbon dioxide in the atmosphere. Clearly the values of these various components will vary with meteorological and topographical conditions and the figures given in Table 5 have been chosen as approximate values for the radiation falling on a body above a grass surface within 2 hr. of noon on a summer day with little or no cloud in southern England.

The long-wave radiation from any surface at 30–50°C. is about 55 mW./cm.²,
but that from a surface facing towards the ground is conveniently set against the radiation from the ground as the net exchange depends more on the difference of temperature between ground and body than upon the actual temperature of either. The figure of 10 mW./cm.² given in the table is for a temperature difference of 20°C, the ground being hotter than the body. This is a fairly high figure, but even so this item of radiation makes a very small contribution to the total balance.

The mean net radiation load per unit surface area of any body will depend, not only upon external conditions, but also upon its own shape, orientation and reflectivity. The effect of these factors can be shown as follows. Fig. 6 gives the net radiation load falling on horizontal, vertical and 45°-inclined plane surfaces under conditions when the figures of Table 5 apply; and these data have been used to construct Table 6 which shows the mean net radiation per unit surface area falling on three widely different rectangular shapes orientated horizontally and obliquely, and with a reflectivity to solar radiation of 0 and 50%. The sun's altitude is 45°; in the horizontal orientation the plane of the sun is perpendicular to one vertical face (a side in the case of the bar), and in the oblique orientation one face (an edge of the plate and an end of the bar) is normal to the sun.

These examples show that the mean radiation load of a body with markedly unequal faces may be varied by a factor of two by re-orientation, the mean of the two extremes being approximately the radiation load of a body with equal faces which is only slightly affected by re-orientation. The examples also show that changes in reflectivity to solar radiation (reflectivity to long-wave radiation being unaffected) produce proportionate changes in the mean radiation load. Data given by Rucker (1933) show the reflectivity of twenty-one insects (mostly beetles) as
varying between 50% (with one example, a white beetle, as high as 74%) and 10%, with a mean of 22%.

(iii) Convection. Convective heat loss from a body surrounded by cooler air is due to the heating of the air and its subsequent removal by currents, and is either natural or forced convection depending on whether the currents are entirely due to density changes consequent upon the heating or whether they are due to an external cause (e.g. wind). Natural convection is likely to be rare in nature, especially under the conditions now being considered when insolation of the ground causes instability in the air and consequent turbulence. The convection coefficient for forced convection (mean heat exchange per unit area per unit difference in temperature between surface and on-coming air) for a body of given shape and orientation with respect to the wind, depends upon the absolute size of the body, the wind speed and the physical properties of the air, according to an expression (McAdams, 1942; Fishenden & Saunders, 1950) of the form:

\[
\frac{\text{Convection coefficient} \times \text{linear dimension}}{\text{Air conductivity}} = a \left( \frac{\text{Air speed} \times \text{linear dimension}}{\text{Kinematic viscosity of air}} \right)^b,
\]

where \(a\) and \(b\) are constants over limited ranges of the Reynolds Number (i.e. the right-hand bracket), \(b\) being less than one. Thus the convection coefficient varies directly as a fractional power of the wind speed and inversely as a fractional power of the linear dimension of the body. This is illustrated by Fig. 7 (data from McAdams, 1942, p. 221), which shows the effect of wind-speed and size upon convective heat loss from a cylinder (wind blowing across the cylinder). From the definition of the convection coefficient (\(h\)) it will be seen that \((100/h)\) (plotted as the ordinate) is the difference in temperature between cylinder and air at which the mean heat loss by convection is 100 mW./cm.² of surface. Fig. 7 thus indicates directly that for a series of cylinders of decreasing size, subject to the same radiation load (and therefore, at equilibrium, losing heat at the same rate per unit area), the equilibrium temperature will decrease with the size of cylinder. It has already been shown experimentally that this is the case for disks of different size (see Fig. 4) and in these

<table>
<thead>
<tr>
<th>Orientation</th>
<th>Reflectivity (%)</th>
<th>Cube (mW/cm.²)</th>
<th>Plate (sides 1:8:8) (mW/cm.²)</th>
<th>Bar (sides 1:1:8) (mW/cm.²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td>0</td>
<td>42</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>19</td>
<td>22</td>
<td>23</td>
</tr>
<tr>
<td>Oblique</td>
<td>0</td>
<td>35</td>
<td>25</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>15</td>
<td>10</td>
<td>9</td>
</tr>
</tbody>
</table>

Table 6. Mean net radiation load for three rectangular shapes
results the apparently linear relation between size and temperature is most likely due to the small range of size considered and not to any fundamental departure from a power law of the type given above.

(iv) Conduction. For the purpose of the measurements described earlier, conduction between body and supports was reduced to insignificant proportions. No information has been obtained about the conduction between animals and their substrate, but it may be taken that as a general rule this is small, especially for arthropods whose hard exoskeleton results in poor thermal contact. This is not to deny, however, that an animal might press itself against a yielding surface and make good thermal contact, and under these circumstances direct conduction would cause the animal’s temperature to approximate to that of the substrate itself.

![Figure 7](image-url)

Fig. 7. Effect of size and wind-speed on the temperature difference between a cylinder and the air when the convective heat loss is 100 mW./cm.² (data from McAdams, 1942, p. 231).

(v) Metabolism. For the present purpose it is necessary to express metabolism in terms of surface area, and whereas many measurements have been made of metabolism (usually rate of oxygen intake) per animal or per unit mass, determinations of area are rare. Butler & Innes (1936) measured the area and oxygen consumption of migratory and solitary L. migratoria, and their results varied from 0.0004 to 0.0011 cm.³ O₂/cm.²/min., which is equivalent to a heat production (at 4.775 cal./cm.³ O₂) of 0.133–0.366 mW./cm.². Gunn (1935) found the oxygen consumption of three species of cockroach to lie between 1.1 and 1.6 mg./cm.²/day at 30° C. and the equivalent heat production is 0.197–0.286 mW./cm.². A rate of heat production of this order is quite insignificant compared with the radiation load.
considered above. Metabolism may rise a hundred times or more during flight, but with this we are not now concerned.

(vi) Evaporation. Despite the amount of attention which has been devoted to the humidity relations of terrestrial arthropods, particularly insects, very little information seems to be available concerning the mean rate of evaporation per unit surface area in natural conditions, particularly for species which normally expose themselves to the sun. Observations made in the laboratory are not directly applicable to the conditions now under consideration, because in the laboratory animals are at approximately the same temperature as the air into which they are evaporating, whereas in the sun they may be considerably warmer than the air. Use can, however, be made of the fact (Ramsay, 1935a) that evaporation rate is proportional to \((p_0 - p_d)\) where \(p_0\) is the vapour pressure of air saturated at the temperature of the surface, and \(p_d\) is the vapour pressure of the 'free' air some distance away. In laboratory observations when the animal is at approximately the same temperature as the air, \((p_0 - p_d)\) is equal to the saturation deficiency; in a typical case of an animal warmed by sunlight to 35° C. in air at 20° C. and 50% relative humidity, \((p_0 - p_d)\) is equal to 34 mm. Hg. Thus the cockroach, Periplaneta americana, which loses water at 6-o mg./hr., or about 0-6 mg./hr./cm.², into air at 20° C., 12-0 mm. sat. def. and 10 m./sec. velocity (Ramsay, 1935b), would be expected to evaporate at \(\frac{34}{12} \times 0.6 = 1.7\) mg./hr./cm.² in the circumstances just specified. Similarly, evaporation from three species of cockroach (Gunn, 1935) into still air would be about 0-4 mg./hr./cm.², and that from a freshly engorged tick, Ixodes ricinus (Lees, 1947), would be 0-65 mg./hr./cm.². Now an evaporation rate of 1 mg./hr./cm.² involves a heat consumption of 0-67 mW./cm.² so that even if water was lost at four or five times the above rates, the corresponding heat consumption would make a barely significant contribution to the total heat balance of an animal being warmed by the sun.

This conclusion is not, however, to deny that under exceptional circumstances, when an insect's spiracles are fully open (Mellanby, 1934) and perhaps the cuticle has passed its critical temperature (Ramsay, 1935; Wigglesworth, 1945), evaporation might affect the equilibrium temperature at least for a short time. This is borne out by observations on grasshoppers (Gunn, 1942) where it was found that when moist air at 35° C. was replaced by dry \((p_0 - p_d = 40\) mm. Hg) the body temperature fell about 4° C., which represents an evaporation rate of about 4-5 mg./hr./cm.² (natural convection coefficient for a cylinder = \(\frac{0.42 \Delta t^{1.25}}{d^{0.25}}\) mW./cm.²/° C., where \(d = \) diameter (McAdams, 1942, p. 241)).

**Heat balance for a body in free air**

Data have been given earlier (Table 1) of the equilibrium temperature of a ½ in. disk suspended 30 in. from the ground on a clear summer day. Temperatures between 9 and 20° C. were obtained. In the absence of simultaneous measurements of solar radiation, atmospheric radiation, ground temperature and mean wind speed, it is not possible to draw up an accurate heat balance. However, it is worth while
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...make a rough estimate of the expected equilibrium temperature and compare it with the observations.

**Radiation.** The figures given in Table 5 for the various components of the radiation exchange between a body and its surroundings were chosen to be applicable to the conditions under which the results reported in Table 1 were obtained. The mean net radiation load on a horizontal black disk (diameter = thickness \( \times 6 \)), calculated from these figures in the way demonstrated for rectangular bodies, is 50 mW./cm.\(^2\).

**Convection.** In the absence of published data on the convection coefficient for small disks at low wind-speeds, some original determinations were made (see Appendix), and the results were as follows:

<table>
<thead>
<tr>
<th>Wind speed (cm./sec.)</th>
<th>50</th>
<th>100</th>
<th>200</th>
<th>400</th>
<th>500</th>
</tr>
</thead>
<tbody>
<tr>
<td>Convection coefficient (mW./cm.(^1)/° C.)</td>
<td>1.4</td>
<td>2.0</td>
<td>2.7</td>
<td>3.8</td>
<td>4.0</td>
</tr>
</tbody>
</table>

**Equilibrium temperature** \((\Delta t)\). This is given, in ° C. above that of the surrounding air, by the expression

\[ R = h_c \Delta t, \]

where \( R \) = mean net radiation load (mW./cm.\(^2\)), \( h_c \) = convection coefficient (mW./cm\(^2\)/° C.). Values of \( \Delta t \) for different wind speeds at \( R = 50 \) mW./cm.\(^2\) are:

<table>
<thead>
<tr>
<th>Wind speed (cm./sec.)</th>
<th>50</th>
<th>100</th>
<th>200</th>
<th>400</th>
<th>500</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Delta t ) (° C.)</td>
<td>36</td>
<td>25</td>
<td>19</td>
<td>13</td>
<td>12.5</td>
</tr>
</tbody>
</table>

To associate these wind-speeds with everyday experience it is useful to note that according to the Beaufort scale (Meteorological Observer’s Handbook, 1942):

<table>
<thead>
<tr>
<th>Scale no.</th>
<th>Direction shown by smoke drift but not by vane</th>
<th>Felt on face; leaves rustle, wind vane moved</th>
<th>Leaves and small twigs in constant motion; light flag extended</th>
<th>Raises dust and loose paper; moves small branches</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Speed at 6 m.\(^*\)

\( \text{cm.}/\text{sec.} \)

<table>
<thead>
<tr>
<th>Scale no.</th>
<th>Speed at 6 m.(^*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>60–170</td>
</tr>
<tr>
<td>2</td>
<td>180–330</td>
</tr>
<tr>
<td>3</td>
<td>340–520</td>
</tr>
<tr>
<td>4</td>
<td>530–740</td>
</tr>
</tbody>
</table>

\(^*\) Speed at 1 m. = \( \frac{4}{4} \) speed at 6 m. (Best, 1935).

On the occasions when the observations on equilibrium temperature in free air (Table 1) were made there was a gustiness in the wind characteristic of the period about noon on sunny days (Sutton, 1949, p. 15). This made estimations of wind speed particularly difficult, but it most likely was between nos. 2 and 3, or 145–420 cm./sec. at a height of 1 m. This is confirmed by Meteorological Office statistics (Observatories Year Book, 1927) which show that in June-August 1925 at Kew Observatory on days when the sun was out at least nine-tenths of the hour ending at noon, the mean wind for that time was 370 cm./sec. at 20 m. which is a little under 300 cm./sec. at 1 m.

At a wind-speed of 150–420 cm./sec. the expected equilibrium temperature according to the above calculation is 22–12° C. which is in good agreement with the observed range of 20–9° C. considering the rough nature of the calculation.
Conditions close to the ground

The principles dealt with above apply equally to animals close to the ground, except that over distances in the order of a millimetre conduction across the layer of air between ground and under surface of body becomes significant, and at the same time air-flow over the under surface is reduced and convective losses consequently fall. However, the actual heat balance and equilibrium temperature in any given case, besides depending on the climatic and morphological factors already discussed, will also depend on so many details of microtopography that only the widest generalization is possible.

As a body approaches a surface warmed by radiation there will be an increase in air temperature and a decrease in wind-velocity while the net radiation load remains the same; hence the equilibrium temperature will rise. The profile of wind and temperature depends on the amount of turbulence in the air: natural surfaces are always more or less rough, causing wind and temperature to change slowly with height except very close to the surface itself. However, most small animals live within the 'roughness', and it is here that conditions are most complex and variable. Wind, and therefore convective loss, is likely to be low, and when the sun can reach the ground to warm it up the temperature profile will be very steep. These conditions prevailed during the observations on the black disk among grass when a temperature change of 12°C occurred over a vertical distance of 1 in. But with thicker vegetation most of the solar radiation is intercepted before reaching the ground by surfaces which are better cooled than the ground itself; and thus the air temperature is lower and has a maximum somewhere between ground-level and the top of the vegetation, and an animal's temperature will follow this profile as was found in observations with the 'artificial lawn' (Fig. 2b).

CONCLUSIONS

The temperature of arthropods in sunlight is determined by the balance between radiative and convective heat exchanges, compared with which the heat associated with metabolism and evaporation is normally insignificant. The radiation load is made up of short-wave radiation received from the sun, directly, diffusely from the sky and by reflexion from the ground; and an exchange of long-wave radiation between the animal and its surroundings, including the atmosphere. The heating due to solar radiation is affected by the colour of the animal, and there may be variations up to 50% in the total radiation load due to this factor alone. The total mean radiation load per unit area will also depend on the shape of the body, and for bodies (such as most arthropods) with markedly unequal surfaces, it may be affected up to about 50% by changes in orientation. The net gain or loss of long-wave radiation is made up of a loss of heat to the atmosphere due to its having an equivalent temperature of approximately 0°C, and a small heat exchange with the ground due to the difference of temperature between it and the animal. Screening the sky by vegetation will reduce the net loss of heat to the atmosphere but will at the same time reduce diffuse solar radiation, so that the resultant effect of changes in the radiation conditions are unlikely to affect the heat balance significantly.
Convective heat loss depends upon the shape of the animal, the wind-speed and the animal's orientation to it, and for a given shape, orientation and wind it also varies inversely as a fractional power of the linear dimension. This means that in any given conditions the smaller an animal is the lower will be the temperature at which convective heat loss balances the radiation load.

It will be evident that the factors determining the temperature of an animal in sunlight, even though they may be reduced to radiation and convection, are very complex and difficult to measure, so that even in the simple case of an animal suspended in free air above the ground a calculation of its temperature will only be very approximate. On the other hand, the insignificance of the 'biological' factors of metabolism and evaporation implies that the temperature of a living animal in a particular situation is likely to be very similar to that of a model of the same approximate size, shape, colour and orientation. Such a model, constructed so that its temperature can easily be measured, may be looked upon as a type of thermometer giving information of considerable biological significance.

When the sun is strong an arthropod, unless it is very small, has at its command temperatures which equal or exceed those of a warm-blooded animal. It remains to be considered to what extent such temperatures are necessary to some animals, and to what extent they are prohibited by the accompanying high rate of evaporation and so represent an important constraint upon the evolution of the habits of terrestrial arthropods. It has already been remarked that, despite the extensive literature on the water relations, particularly of insects, no information seems to be available concerning the rate of evaporation in natural habitats where the animal may be warmed considerably above air temperature, where local humidity, no less than temperature, may be very different from what is reported by the meteorologist, and where sources of water may be available to replenish what is being lost.

**SUMMARY**

1. A study has been made of the factors determining the temperature of terrestrial arthropods in sunlight.

2. For such animals the most important forms of heat exchange, which determine the equilibrium temperature, are radiation and convection. Compared with these, evaporation and metabolism are insignificant except under unusual circumstances.

3. Convection depends on the size of the body in such a way that the temperature of similar animals in similar circumstances will vary as about the square root of the linear dimension. Other morphological features affecting temperature are shape, orientation and colour.

4. The factors on which such animal temperatures depend are difficult to measure, and it is unlikely that temperatures will ever be accurately deduced from heat-balance considerations. But the insignificance of metabolism and evaporation implies that the temperature of the living animal in a given situation is likely to be very similar to that of an inanimate body of the same approximate size, shape, colour and orientation. If the temperature of such a body can be measured it forms a type of thermometer giving information of direct biological significance.
5. Terrestrial arthropods may be as warm as, or warmer than, the 'warm-blooded' animals, particularly on the ground where conditions change rapidly over small distances so that animal temperatures must be profoundly affected by behaviour.

6. Laboratory data on evaporation at high temperatures do not apply directly to conditions in the field, because an animal warmed by the sun will not necessarily lose water at the same rate as one warmed to the same temperature by warm air at the same relative humidity.

Among several people with whom I have discussed aspects of this work I should particularly like to thank Dr M. Fishenden (convection) and Mr N. E. Rider (atmospheric radiation). I am also indebted to Dr R. H. J. Brown for advice on the construction of the thermistor recorder.

APPENDIX

Natural and forced convection from small disks

Published data on convection is almost entirely limited to wires and cylinders, spheres and large surfaces. The convection coefficients for small disks used in the present paper were original determinations made on a $1 \times \frac{3}{8}$ in. brass disk fitted with a nichrome-constantan thermocouple and a nichrome heating coil of known resistance through which a range of known currents was passed. Natural convection measurements were made in a small sound-proof room almost completely free from draughts; and forced convection measurements were made in an 18 x 30 in. wind-tunnel, the disk being suspended by the thermocouple wires 9 in. from the nearest side. The wind-tunnel had a straight entry with a $5 \times 5$ mm. grid of 1 mm. wire 200 cm. upwind from the disk. Wind-speed was calibrated against propeller r.p.m. by timing smoke puffs.

Calculation. The apparent convection coefficient ($h'_c$) is given by

$$H = \varepsilon A \sigma (T_d^4 - T_a^4) + h'_c A (t_d - t_a),$$

where $H$ = heat input ($I^2R$), $A$ = area of disk (12 cm.$^2$ including edges); $\varepsilon$ = emissivity, taken as 0.2 when unpainted and 0.95 when matt black; $\sigma$ = Stefan-Boltzmann constant; $t_d$, $T_d$, $t_a$, $T_a$ = temperature in °C. and °Abs. of disk and air.

This ignores heat loss down the thermocouple and heater wires. For a uniform wire one end of which is at temperature $t_d$ and the other at air temperature $t_a$, the heat loss by convection is given by (Ingersoll, Zobel & Ingersoll, 1948, p. 21):

$$H_w = \frac{1}{\pi} (t_d - t_a) \sqrt{kd^3h_w},$$

which is of the form

$$H_w = h'_w (t_d - t_a),$$

where $k$ = conductivity of wire, $d$ = diameter of wire, $h_w$ = convection coefficient of wire. Thus the true convection coefficient ($h_c$) of the disk is given by

$$H = \varepsilon A \sigma (T_d^4 - T_a^4) + h_c A (t_d - t_a) + h'_w (t_d - t_a).$$

From (1) and (2),

$$h_c = h'_c - \frac{h'_w}{A}. $$

The heat loss down the heater wires was ignored because of their fineness (48 s.w.g.)
Temperature of terrestrial arthropods in sunlight

*And low heat conductivity. Values of $h'_w$ for the thermocouple wires were calculated as follows, using data on $h_w$ given by McAdams (1942, p. 229):

<table>
<thead>
<tr>
<th>Wire gauge</th>
<th>$h_w$</th>
<th>$h'_w$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>25 cm./sec.</td>
<td>200 cm./sec.</td>
</tr>
<tr>
<td>40 s.w.g. constantan</td>
<td>0.15</td>
<td>0.23</td>
</tr>
<tr>
<td>43 s.w.g. nichrome</td>
<td>0.08</td>
<td>0.12</td>
</tr>
<tr>
<td>48 s.w.g. nichrome</td>
<td>0.03</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Thus at 25 cm./sec. $h'_c = h'_c - \frac{0.23}{A} \approx h'_c - 0.02$,

200 cm./sec. $h'_c = h'_c - \frac{0.35}{A} \approx h'_c - 0.03$.

In the present calculations a correction of 0.03 mW/cm.$^2$ was applied. It is not possible to apply a similar correction to the measurement of natural convection, but the correction factor is likely to be less than 0.02 mW/cm.$^2$.

Results

Natural convection. Seven determinations of the natural convection coefficient were made over the range 22.6–11.7°C (mean = 16°C) temperature difference.

![Graph showing convection coefficients of a 1 x 1/4 in. disk at various wind-speeds.](image-url)
between the disk and air, the mean film temperature being 28.9°C. The mean coefficient was 0.67 ± 0.03 mW./cm²°C, the mean log (Gr x Pr) number being 4.38 and the mean log (Nu) number being 0.82. These figures are in good agreement with those given by Fishenden & Saunders (1950, p. 95) for a horizontal plane surface facing upwards.

**Forced convection.** The forced convection coefficient at different wind-speeds are shown in Fig. 8. The good agreement between the values obtained with a polished and a blackened disk supports the assumed values of the emissivity in the two cases. The range of \(2.5 \times 10^2\) to \(5.0 \times 10^3\) in the Reynolds Number is too small to give anything but a very rough indication of the relation between this and the Nu Number. From the data available the relation appears to be

\[ \text{Nu} = 0.6 \times \text{Re}^{0.47} \]

This is remarkably close to the relation for cylinders for these Reynolds Numbers which is (Fishenden & Saunders, 1950, p. 130)

\[ \text{Nu} = 0.615 \times \text{Re}^{0.436} \]

**REFERENCES**


