

THE BODY TEMPERATURE OF WOODLICE

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(Received 17 November 1950)

(With Four Text-figures)

INTRODUCTION

The present work forms part of an investigation into the water relations of woodlice. It has already been shown (Edney, 1951) that, during short exposures, woodlice can tolerate a higher temperature if the air is dry than if it is saturated with water vapour, and the experiments to be described were designed to estimate more precisely the effect of evaporation of water on the body temperature of the animals concerned. Measurements of the body temperature of insects under various environmental conditions have been made by several workers and reviewed by Gunn (1942), but no comparable data for woodlice are available, and since they apparently lack the efficient waterproofing layer in the integument which is characteristic of the majority of terrestrial insects, they might be expected to show greater temperature effects due to evaporation.

METHODS

In measuring the temperature of small animals such as woodlice, the instruments themselves may introduce considerable error. Where thermocouples are used, as in the present work, the two main sources of error are the risk of damage to the animal and conduction of heat by the instrument, and for these reasons the usual thermoneedles are unsatisfactory. It is not possible entirely to avoid error, but the amount can be greatly reduced if the instrument used is small and smooth, and this was aimed at in the construction of the thermocouples used in the present experiments. The junctions were made of 48 s.w.g. copper and constantan wire and coated with bakelite varnish. The wires were silver-soldered together end to end. This can be done, using a binocular microscope and a very small gas jet, so that there is no appreciable increase in the diameter of the wire. The joined wire is then coated with varnish and baked, after which the wires are bent at the joint so that they lie parallel. A short piece of narrow-bore glass tubing slipped over the two wires and varnished into position leaving rather less than 1 cm. projecting with the junction itself at the tip, provides a useful hold for the forceps when inserting the thermocouple and a protection against damage to the insulating varnish.

As regards the accuracy of this instrument, Shakespeare (*in litt.*) has shown empirically that where a thermojunction composed of 46 s.w.g. copper and constantan is immersed in a body whose temperature is 35° C. higher than that of the air through which the junction wires run, conduction of heat away from the body by the wires will not lead to an error greater than 0.01° C. provided the junction is at least 2.0 mm.

inside the body. (Empirical data for large thermo-needles were determined by Gunn *et al.* (1948).) In the present experiments, conditions were well within these limits, so that errors in temperature as a result of conduction by the thermocouple wires can safely be neglected.

The apparatus used is shown diagrammatically in Fig. 1. The experimental chamber itself is a glass vessel, 2.5 in. in diameter and 4 in. long, through which a stream of air can be passed. At the outlet end a large rubber bung carries a glass tube through which air is extracted by a small pump (*P*). The air is then dried and brought to the required temperature by passing through a copper coil which is immersed in a tank of water together with the experimental chamber, the temperature of the water being controlled to within 0.1° C. The air then re-enters the experimental chamber. Inside the chamber a perspex framework attached to the bung

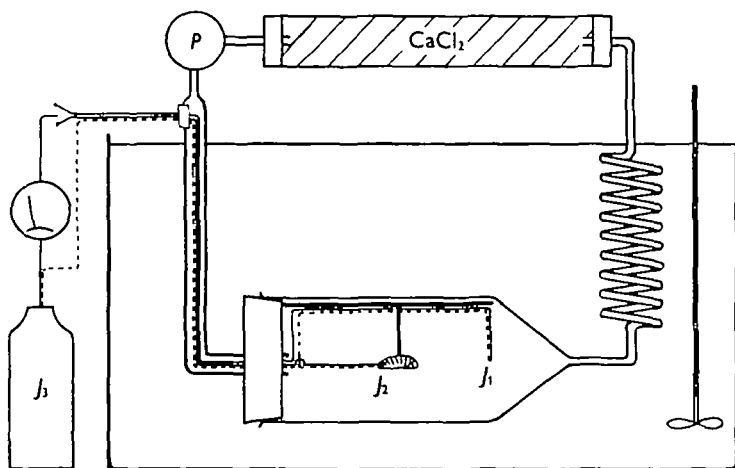


Fig. 1. Apparatus used for measuring the temperature of woodlice under controlled conditions. J_1 and J_2 , thermojunctions in the oncoming air and the animal respectively; J_3 , constant-temperature junction; P , air pump.

carries terminals for the fine thermocouple wires and an arm for holding the animal during an experiment. There are two thermojunctions inside the experimental chamber, the first (J_1) is supported in front of the animal in the advancing air stream, the second (J_2) is inserted into the rectum of the animal, the latter being held by a loop of thread which emerges from the hollow supporting arm and which can be adjusted from outside the chamber. (This thread is not shown in the diagram.) From the terminals mentioned above, thicker insulated wires (two copper and one constantan) run through the glass tube to above water-level, where they emerge through an air-tight joint and run to the 'cold junction' (J_3) and galvanometer. The cold junction used was a large thermos flask of water at 17° C. There was no noticeable change in the temperature of this junction as measured by a mercury thermometer in as long as 12 hr., and since an experiment usually lasted for about 1 hr., the constancy of the cold-junction temperature can be assumed. By means of a simple

switch either junction \mathcal{J}_1 or \mathcal{J}_2 can be brought into circuit. Air was pumped round the circuit at 1 l./min.

In experiments such as these, the value of the results is of course limited by the accuracy of the measuring instruments. Many thermojunctions were made; each was calibrated separately, and no junction was used unless during calibration it was free from hysteresis for either rapidly or slowly changing temperatures and gave repeatable readings within 0.1°C . During calibration the junction was immersed in stirred water whose temperature was read by a mercury-in-glass thermometer graduated to 0.1°C .

Before experiment, the animals were all kept at room temperature in a saturated atmosphere. The animal to be used for experiment was lightly anaesthetized with ether to facilitate handling; the thermocouple junction was then inserted into the rectum through the anus for a distance of about 4 mm. If any sign of damage to the animal was visible as a result of this insertion, it was discarded and another animal used. (With practice it was usually possible to insert the junction easily and without apparent damage.) The animal was then attached to the holder, either by a drop of wax or by the fine thread described above (the procedure used made no difference to the results); the rubber bung with its attached frame carrying thermojunctions and animal was then inserted into the glass chamber and the whole immersed in the tank of water. Air of the required temperature and humidity was then allowed to flow past the animal (rate of flow 1 l./min.), and the temperatures of the oncoming air and of the animal were read every 2 min. or every 5 min. according to the nature of the experiment.

If the animals were alive when exposure commenced they would usually remain alive during a 45 min. exposure, except in dry air at 37°C . There was, however, no difference in amount of cooling between living and dead animals, so that this factor can safely be neglected.

EXPERIMENTAL RESULTS

(a) *The effect of warm dry air on the temperature of Ligia*

The first experiments were carried out on *Ligia*, the largest of the British terrestrial isopods. Dry air at 30°C . was used in these experiments. After the temperature of the animal had reached its lowest point, the dry air was replaced by saturated air which had been bubbled through a series of vessels containing water at the same temperature as the air inside the chamber. After the temperature of the animal had again settled down (11 min.), dry air was once more introduced to replace the moist.

Fig. 2 is a composite curve derived from several such experiments—the initial period of equilibration is not shown. During the first 'dry' period, the lowest body temperature of the animal was 6.2°C . (mean of four determinations, varying from 5.9 to 6.4°C .) below that of the surrounding air at 30°C . As soon as saturated air was introduced, however, the temperature of the animal rose rapidly until it reached the same temperature as the surrounding air. During the second 'dry' period the temperature again fell, rather more slowly than it had risen, and not quite so far as in the first dry period.

This experiment was repeated using a dead animal with results which were so similar to those from the living animal as to make a second curve unnecessary.

(b) *A comparison with other species of woodlice*

Data derived from the type of experiment described above are satisfactory in providing a general picture of what is going on in the particular animal used, but the information is too qualitative for comparisons to be made between one species and another. Data derived from experiments in which the temperature of the air rises (several such experiments were done) are also unsatisfactory in this respect, since it is not easy to control the rate of rise of temperature, and there is no means of telling

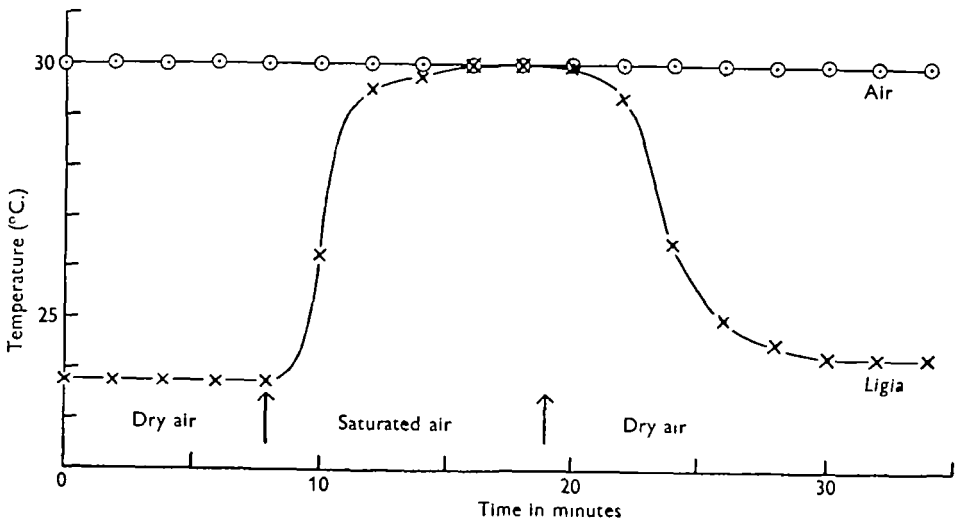


Fig. 2. Temperature curve for living or dead *Ligia* exposed to slowly moving air at 30° C.

to what extent, owing to its thermal capacity, the temperature of the animal lags behind that of the air.* The best one can do towards making quantitative comparisons between species is to use a constant temperature and humidity, and to choose an arbitrary time after the commencement of the experiment (when each species is giving fairly constant readings), at which to measure the cooling effect.

Experiments with this end in view were carried out using *Armadillidium vulgare*, *Oniscus asellus*, *Porcellio scaber*, *Ligia oceanica*, and the insect *Blatta orientalis*. In one series of experiments a constant air temperature of 37° C. was used, in another, 20° C., and the air was dry. The experiment was repeated with at least three individuals of each species as alike in size as possible. In another series individuals of each species were subjected to the same treatment except that the air was saturated with water vapour. In all these experiments readings were taken every 5 min. and continued until the temperature had settled down for at least 10 min. This meant an exposure of about 40 min. for all species except *Ligia* whose temperature did not settle down even after 2 hr. exposures.

* See discussion on p. 278.

The results are shown in Table 1, and a selection of them are graphed in Figs. 3 and 4. The curve shown for any one species is the curve for that specimen which, by reason of its central position, is most representative of the group. An indication of the variation encountered is shown, where relevant, by vertical lines at the end of each curve; this represents the variation at that time and does not necessarily correspond in all cases with the variation shown in Table 1 which is based on readings taken 30 min. after the commencement of each experiment.

Table 1. *Depression of body temperature below that of a surrounding stream of air at either 20 or 37° C., after 30 min. exposure*

	Air temperature 20° C.				Air temperature 37° C.			
	No. of observations	Depression in ° C.			No. of observations	Depression in ° C.		
		Mean	Max.	Min		Mean	Max.	Min.
<i>Ligia</i>	3	2.6	3.0	2.3	3	6.8	7.3	6.8
<i>Omscus</i>	3	1.5	1.6	1.3	3	2.7	3.0	2.5
<i>Armadillidium</i>	3	0.5	0.5	0.4	4	1.8	2.0	1.5
<i>Porcellio</i>	3	0.4	0.4	0.3	4	1.3	1.5	1.1
<i>Blatta</i>	3	0.7	0.7	0.6	3	2.4	2.4	2.3

The position on the ordinate from which each curve runs is, of course, quite without significance for the present purpose; it depends merely upon the temperature of the animal when the first reading was taken, which may have been anything up to 2 min. after assembly of the animal in the apparatus.

It is clear from these curves that the arbitrary time of 30 min. after the beginning of an experiment chosen for the comparative figures given in Table 1 is not entirely satisfactory; the temperature of *Ligia*, for example, continues to rise slowly throughout the experimental period, and that of *Blatta* at 37° C. is not quite steady. However, all the other species used give constant readings from about 25 min. onwards, so that the comparison is worth making.

In all experiments where the air was saturated, the temperature of the animals was, within the limits of accuracy of the apparatus, the same as that of the air, so that the depressions of temperature in dry air are certainly due to evaporation. Since they are all the same, the curves for saturated air are not shown in the figures.

When the depressions shown by each species are compared, it is apparent that the amount varies considerably from one to another, and that the depression is greater when the air temperature is 37° than when it is 20° C. *Ligia* shows by far the greatest depression, as much as 7 from 37° C.; next comes *Omscus*, while *Armadillidium* and *Porcellio* show the least depression. The order of the species is the same at both temperatures, and corresponds with the order as regards rate of evaporation which was found previously (Edney, 1951), with the exception of the relative positions of *Armadillidium* and *Porcellio* at 37° C.; but at that temperature, both the evaporation rates and temperature depressions of the two species are close together, so that little significance can be attached to their relative positions. These results are discussed further below.

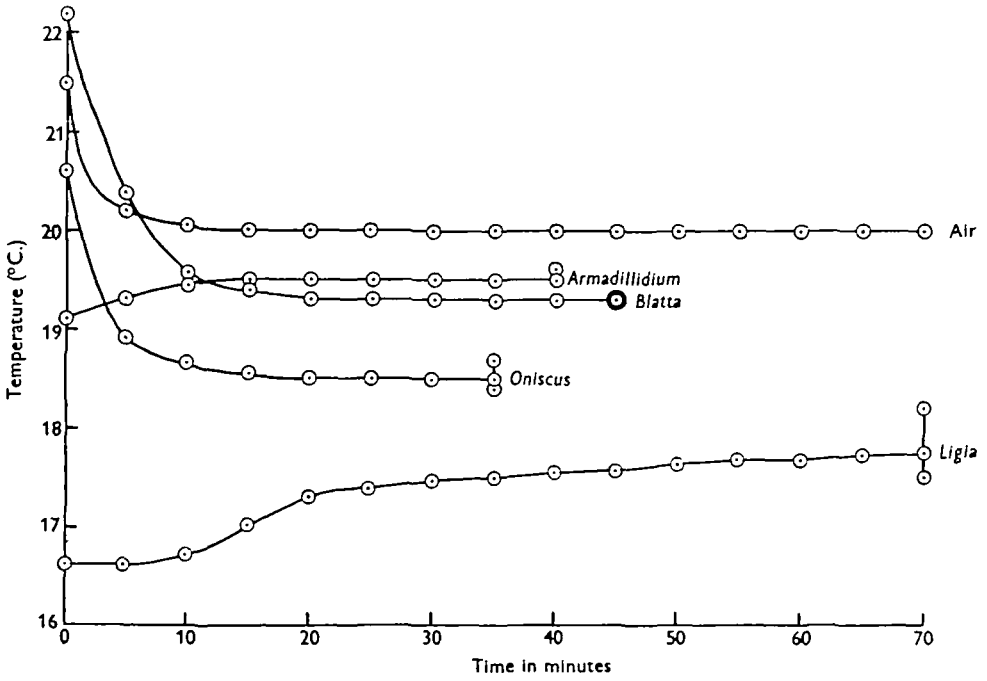


Fig. 3. Temperature curves for various woodlice and the cockroach, *Blatta*, exposed to slowly moving dry air at 20° C.

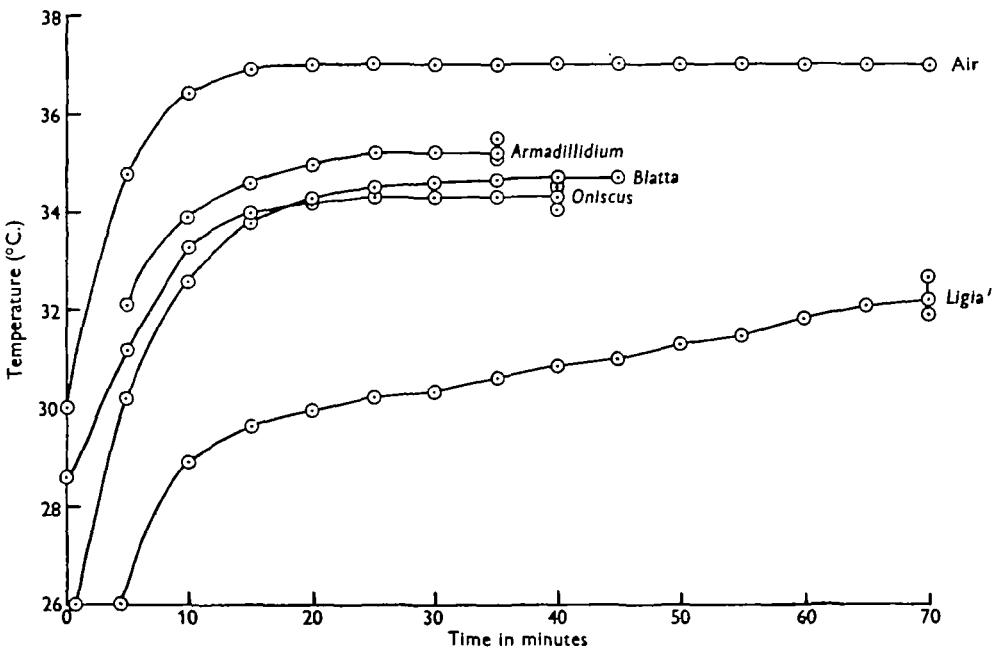


Fig. 4. Temperature curves for various woodlice and the cockroach, *Blatta*, exposed to slowly moving dry air at 37° C.

It is interesting to notice that the insect *Blatta*, which is approximately the same size and shape as *Ligia*, shows a very much smaller temperature drop than the latter, an observation which corresponds with what is known of the permeability of the insect cuticle as compared with that of woodlice.

Direct estimation of the water lost during some of these experiments was made by weighing the animals before and after exposure. At 20° C. a specimen of *Ligia* which showed a temperature depression of 2.6° C. lost 0.06 g. water/hr., while an *Armadillidium* which showed a temperature drop of 0.4° C. lost 0.002 g. water/hr. *Ligia*, therefore, lost thirty times as much water as *Armadillidium*, and its surface area was only five times greater, so that the rate of evaporation per unit area was six times greater from *Ligia* than from *Armadillidium*, and a more pronounced drop in temperature was to be expected. Another such comparison was made between *Ligia* and *Blatta* at 37° C. The dimensions of the two animals were approximately the same, yet *Ligia* lost two and a half times as much water as *Blatta*, and its temperature depression was correspondingly greater (6.8° C. as compared with 2.4° C.).

DISCUSSION

The experiments described have shown a depression in the body temperature of woodlice below that of the environment. Results of this kind may be considered from two points of view: first, they provide biophysical information relating to permeability of the integument and allied phenomena, and secondly, they provide ecological information concerning the distribution and evolution of woodlice. Considered biophysically it is important to know just what physical or physiological factors produce the temperature depressions recorded; considered ecologically, the precise interplay of causes is not so important as the aggregate effect. The present results will be considered from the biophysical aspect first.

When, during the course of an experiment, a steady temperature is reached, total heat lost by the animal must be equal to total heat gained. Heat is gained from the environment by radiation and conduction, and from within by metabolic heat. Under the conditions used, heat gained by metabolism is unimportant, for if metabolic heat contributed significantly to the balance one would expect to find the temperature of the animal above that of the environment when loss of heat by evaporation was prevented in saturated air. In fact such a rise in temperature was never greater than 0.1° C.

Gain of heat by radiation is an unknown factor, but in all probability it is low. By far the greatest gain of heat is by conduction from the air, conduction by the wires of the thermocouple having been shown above probably to be negligible. Similarly, the only important means by which heat is lost (radiation again being doubtful but probably very low) is evaporation of water from the surface.

It is approximately true to say, therefore, that the final equilibrium temperature reached is that at which heat gained from the air just balances heat lost by evaporation; and since both processes are roughly proportional to surface area, then provided the rates *per unit area* remain constant, the equilibrium point will be independent of size. It can be assumed that, under the conditions used, the rate of gain of heat from

the air is not significantly affected by differences in cuticle structure between one species and another, so that the observed specific differences in equilibrium temperature can be wholly ascribed to differences in rates of evaporation, and species which show greater rates of evaporation may be expected to show greater temperature depressions (although the two variables may not be strictly proportional) no matter what their size.

On the other hand, the speed of equilibration will be slower in larger animals, for the volume (and hence the thermal capacity) of a body of constant shape increases more rapidly with length than does surface area. For this reason, the relative speed of equilibration in various species bears no relation to the permeability of their integuments, and information about the latter can only be obtained by a comparison of equilibrium temperatures.

There are no previous data for body temperatures of woodlice, but the present results may be compared with those obtained for various insects. Several authors, e.g. Necheles (1924), Mellanby (1932) and Koidsumi (1935), have measured the effect of dry air on the body temperature of large insects, and in general they have found temperature depressions of from 3 to 5° C. when air temperatures are high (about 40° C.). Knowing as we do that the permeability of the insect integument is usually a good deal lower than that of woodlice, these figures may appear rather high; but as Ramsay (1935), Wigglesworth (1945) and others have shown, the insect cuticle undergoes a change at temperatures which vary from one species to another (about 35° C. for *Blatella*) leading to much greater permeability, so that large depressions at high temperatures are not unexpected. Even so, the depressions found are not so great as that shown by *Ligia* at 37° C.

Not many measurements of small insects' temperatures have been made—surely the most ambitious attempt is that of Vinogradskaya (1942) who measured the temperature in different parts of the mosquito *Anopheles maculipennis*. She claims to have found a body temperature up to 1° C. higher than the surrounding air between 5 and 25° C., with saturation deficiencies up to 10 mm. Hg. Above 25° C. she finds a body-temperature depression up to 3° C. in dry air. Such temperatures are not, of course, impossible, but they must be extremely difficult to measure accurately.

Another respect in which woodlice differ from some insects is the behaviour as regards temperature depression of dead as compared with living animals. In the present work, no difference at all was found, whereas in insects the temperature depression is often greater in living than in dead individuals. Thus Buxton (1924) found that the temperature of a living *Adesmia* beetle exposed to direct sunlight on sand was only 0.5° C. above the sand temperature, but rose to about 6° C. above if the insect was dead. (Koidsumi (1935), however, found no such difference in the insects with which he worked.) The explanation of this anomaly may lie in the difference between the site of water loss in insects and woodlice; in the former, the greater part of evaporation takes place through the spiracles, and if these are closed after death, evaporation is reduced and the temperature depression is less. In woodlice, on the other hand, the absolute amount of water lost through the respiratory surfaces is not more than a fifth of the total amount (Edney, 1951), evaporation takes

place from the whole body surface, and this undergoes no significant change at death.

Turning now to the ecological implications of the present results, we may ask whether the temperature depressions shown, no matter how they are caused, are of survival value, and if so, whether they are of significance in the evolution of the group.

The impression gained from studying the effect of humidity upon upper tolerable temperature limits, that the ability to evaporate water rapidly will enable woodlice to survive short exposures to temperatures which would otherwise be fatal, is confirmed by the present results. *Ligia* for example is killed by a 15 min. exposure to 34.5° C. in saturated air, but it can withstand 41.5° C. in dry air, and this difference corresponds well with the temperature depression of 7 from 37° C. which has now been measured. The effect is smaller in other genera, but even in *Armadillidium* a depression of 1.8° from 37° C. occurs, and may well be of survival value. If we suppose woodlice to have evolved from maricolous to terricolous forms via the littoral zone, then the capacity to keep cool by rapid evaporation during short periods of exposure to high temperatures would have been of great value, as it may well prove to be in the littoral form *Ligia* to-day. Unfortunately, we do not yet know anything of the precise microclimatic conditions to which woodlice are subjected in the field, so that the picture remains for the present incomplete.*

On the other hand, as compared with insects, woodlice have little real advantage, for although insects usually are not able to cool themselves so much as woodlice by rapid evaporation, they have developed a higher temperature tolerance, and this, so far as adaptation to terrestrial conditions is concerned, is of much greater value.

SUMMARY

1. Measurements by means of thermocouples, accurate to 0.1° C., were made of the body temperature of the woodlice *Armadillidium*, *Porcellio*, *Oniscus* and *Ligia*, and of the cockroach *Blatta*, both alive and dead, in a stream of saturated or dry air at both 20 and 37° C.

2. No difference in temperature depression was found between living and dead woodlice, and in all the animals used there was, after equilibration, no difference greater than 0.1° C. between the air temperature and body temperature if the air were saturated with water vapour.

3. In dry air, the body temperature of all the animals except *Ligia* settled down after at most 25 min. to a steady temperature which was lower than that of the surrounding air. The body temperature of *Ligia* continued to rise slowly for at least 2 hr., though remaining well below that of the environment.

4. After 30 min. in dry air at 20 and 37° C. respectively, mean temperature depressions (of at least three readings at each temperature for each species) were, in degrees centigrade: *Ligia*, 2.6 and 6.8; *Oniscus*, 1.5 and 2.7; *Porcellio*, 0.4 and 1.3; *Armadillidium*, 0.5 and 1.8; and the cockroach *Blatta*, 0.7 and 2.4. The order of the

* Parallel evidence bearing upon differential adaptation to terrestrial conditions has recently been demonstrated in the allied field of excretion by Dresel & Moyle (1950).

species in this respect is substantially the same as their order in respect of evaporation rate, which was established previously.

5. Certain anomalies which appear when these figures are compared with previously established figures for insects are probably the result of differences in permeability of the integument and in the site of water loss. The ability to evaporate water rapidly, and thus to cool the body, may be of survival value when woodlice are exposed to high temperatures for short periods, particularly in littoral forms which may well have been intermediate in the evolution of terricolous from maricolous isopods.

The above work was carried out while in receipt of a grant from the Agricultural Research Council. My thanks are due to Dr J. A. Ramsay for his most helpful observations upon the manuscript of this paper. I am also indebted to Dr G. A. Shakespeare for permission to quote unpublished work, and to Mr R. Priest for his painstaking assistance.

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