THE TEMPERATURE AND HUMIDITY RELATIONS OF THE COCKROACH

III. A COMPARISON OF TEMPERATURE PREFERENCE, AND RATES OF DESiccATION AND RESPIRATION OF PERIPLANETA AMERICANA, BLATTA ORIENTALIS AND BLATella GERMANICA

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(With Two Text-figures.)

Previous studies in this series (Gunn, 1933, 1934) have dealt with certain aspects of the physiology of the common black beetle, Blatta orientalis. The present paper is a comparison of that and two other exotic native species of cockroaches. The smallest of the three, Blatella germanica, is found in hotel kitchens, hospitals and public houses, and most rarely in private houses. Development from hatching to the last moult occupies 3 months at 23° C. (Zabinski, 1929). Blatta orientalis is very common in similar places and also in older houses of the poorer class. Its development occupies 1 year at 23° C. (Zabinski, 1929). Periplaneta americana, the largest species, seems to be found only in the tropical houses in Zoological and Botanical Gardens. The duration of its life cycle appears to be unknown. No reasons have hitherto been given for the existing distribution of these three species. In this paper some contributory reasons are put forward.

In the experiments here described, adult males only were used. P. americana was obtained from a dealer and the other species were caught locally. All animals were kept a few days before use, and were fed on carrot and water in an oven at 25° C.

Desiccation.

The rate of loss of weight of each species was found in dry air at temperatures ranging from 20 to 36° C., using the methods previously described. It was then shown that this rate of loss of weight is a satisfactory measure of the rate of evaporation of water from the animal (Gunn, 1933). The results are shown in Fig. 1 and Table I. The results for Blatta orientalis are taken from the previous work cited. It will be seen that at lower temperatures the two larger species lose water at about the same rate, and that the smallest, Blatella germanica, has a much higher rate of loss. Above 30° C. the rate of loss from the two smaller species increases very
rapidly, while in *Periplaneta americana* the rate rises more uniformly. Further reference is made to this in the discussion.

![Graph showing rate of loss of weight](image)

**Fig. 1.** Rate of loss of weight, which is a measure of rate of evaporation of water, plotted against dryness of the air. In all the experiments the air was dry. Each point represents an average from not less than ten animals.

**Table I. Rates of loss of weight (water) in dry air at the temperature specified.** Each figure is the average loss of weight per day expressed as a percentage of the original weight.

<table>
<thead>
<tr>
<th></th>
<th>20° C.</th>
<th>25° C.</th>
<th>30° C.</th>
<th>33° C.</th>
<th>36° C.</th>
<th>40° C.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Periplaneta americana</em></td>
<td>3.1</td>
<td>5.0</td>
<td>8.6</td>
<td>13.9</td>
<td>21.3</td>
<td>65</td>
</tr>
<tr>
<td><em>Blatta orientalis</em></td>
<td>3.3</td>
<td>6.2</td>
<td>9.5</td>
<td>21.3</td>
<td>55</td>
<td>159</td>
</tr>
<tr>
<td><em>Blatella germanica</em></td>
<td>5.6</td>
<td>9.4</td>
<td>15.9</td>
<td>28.6</td>
<td>60</td>
<td>—</td>
</tr>
</tbody>
</table>

**RATE OF RESPIRATION.**

The rate of oxygen consumption was measured with the Barcroft apparatus as previously described, but in this case at one temperature (30° C.) alone. The figures of oxygen consumption given in Table II (p. 187) are averages from 12–14 specimens of each species. It will be observed that while in these experiments the average rate of oxygen consumption of *Blatta orientalis* was 16 mg./gm./day (live weight),
in the previous ones (Gunn, 1933) it was 13 mg./gm./day at 30° C. When the rate of respiration is measured on successive days, it is found to be high at first and then to decline, day by day (cf. Buxton, 1930). In the experiments of 1933 each animal was used for a fortnight. In the present work only the first day’s rate was taken. The latter method gives a satisfactory figure for comparing species, whereas the former is required for finding a temperature coefficient.

Table II.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. americana</td>
<td>912</td>
<td>13·0</td>
<td>86</td>
<td>8·2*</td>
<td>10·5</td>
<td>1·6</td>
<td>6·6</td>
</tr>
<tr>
<td>B. orientalis</td>
<td>380</td>
<td>16·0</td>
<td>95</td>
<td>11·0</td>
<td>8·6</td>
<td>1·45</td>
<td>5·9</td>
</tr>
<tr>
<td>B. germanica</td>
<td>47</td>
<td>24·1</td>
<td>159</td>
<td>21·9</td>
<td>7·3</td>
<td>1·1</td>
<td>6·6</td>
</tr>
</tbody>
</table>

* From approximate measurements.

TEMPERATURE PREFERENCE.

This part of the work was carried out using the apparatus and methods previously described (Gunn, 1934). In Fig. 2 are shown the results. It will be seen that the upper temperature limit for B. orientalis (29° C.) is lower by 4° C. than it is for the other two species (33° C.). The lower temperature limit is not so sharply defined, and in any case aberrant animals occurred which had a lower preferred temperature.

![Preferred temperature diagram](image-url)
and a greater range than the majority (Fig. 2, A and B). These aberrant animals were not desiccated and no explanation has been found for their different behaviour. Consequently importance can be attached only to the upper limit of range.

**DISCUSSION.**

In the desiccation experiments at lower temperatures the rate of loss of water of the smallest species (*Blatella germanica*), expressed as a percentage of the original weight, was nearly twice that of the largest species (*Periplaneta americana*) (Table I, Fig. 1). This suggests that the water vapour evaporates through the surface of the animal, since if the shape remains constant the smaller the animal the larger the surface area per gram. The surface area is difficult to measure directly, but in similar animals it may be estimated as proportional to weight. In Table II are shown certain relevant figures in this connection, namely the calculated surface area per gram and the water loss and oxygen consumption per unit of surface area. It will be seen that the water loss per unit of surface area is least in the smallest species, which has the least total thickness of integument. From the same table it will be seen also that in all three species about 6 mg. of water is lost for each 1 mg. of oxygen consumed.

Now it is clear from direct experiments that some water escapes from the spiracles of insects (Koidsumi, 1934; Mellanby, 1934) and that some evaporates through the general integument (Koidsumi, 1934). Koidsumi (1934) has shown further that in *Mlitonia* pupae evaporation through the integument does not follow Dalton’s Law precisely and that the loss of water per unit of saturation deficiency rises with rising temperature. Since, then, the insect integument seems not to behave like a simple water surface, it is not possible to draw general conclusions from the experiments here described. But it will be seen from Table II that if the permeability of the cuticle of *Blatella germanica* is the same as or higher than that of the other species, then there must be in *B. germanica* a compensatory higher efficiency in the water conserving properties of the tracheal system, such as might be expected on grounds of size when oxygen reaches the cells by diffusion alone.

In this paper, little has been said about the rapid rise in rate of water loss above 30° C. Through the courtesy of Mr J. Arthur Ramsay, I understand that this rise is not essentially due to the onset of pumping movements, as was previously suggested (Gunn, 1933), although pumping movements do result in a considerable rise. The phenomenon will be discussed by him in a forthcoming publication.

An approximate calculation (assuming r.q. = 0.73) from Buxton’s figures for the mealworm (larva of *Tenebrio*) (1930) shows that in that animal at 30° C. in dry air, the weight of water lost is always less than the weight of oxygen consumed, while in these cockroaches 6 units of water are lost for one of oxygen gained. This suggests that a comparison of the properties of the respiratory systems of the two forms would throw some light on the resistance of desiccation found in the mealworm. For example, the hypothesis that not only the cuticle but also the tracheal walls are impermeable to water vapour and that all the water lost evaporates from
the tracheoles approximately fits the facts for the mealworm, but not for the cockroach (Krogh, 1920; Adler, 1918; Buxton, 1930; Mellanby, 1932).

It will be seen from the table that the rates of oxygen consumption of the three species of cockroaches are proportional neither to the weight nor to the surface area. Actually they are proportional to the weight to the power of 0.75–0.8. It is noteworthy that this same numerical factor (0.75) is found for the homoiothermal mammals (Kleiber, 1933).

In the temperature preference results it would be premature to attempt to attach an ecological significance to the lower limit of the range until some explanation is found for the behaviour of the aberrant animals, but a sharp upper limit of temperature was found for each species. On comparing Figs. 1 and 2 it will be seen that only in Blatella germanica does the animal enter and remain at a temperature at which desiccation takes place rapidly. The highest temperature at which Periplaneta americana will remain when given a choice is below 33°C., and at that temperature the rate of desiccation is about 14 per cent. per day. At the same temperature, which is occasionally preferred by Blatella germanica, the latter species loses water at the rate of 28.6 per cent. per day, and on an average dies in just over 40 hours. At its highest preferred temperature Blatta orientalis loses under 10 per cent. per day. Since all three species can safely stand a loss of 30 per cent. and still recover on drinking, it will be seen that only in the case of Blatella germanica does the temperature preference take the animal into a temperature where it will desiccate to death in under 2 days. These facts are in keeping with the fact that I have never found B. germanica in a place where it could not easily obtain water to drink at least once a day, while Blatta orientalis is sometimes found in living rooms where it would have to walk into the next room to drink. This might easily be a very important factor in the life of the minute newly hatched insect, with a higher respiratory rate and a smaller radius of action. Previous work has shown that the cockroach is protected from fatal desiccation by a change in the reaction to temperature (Gunn, 1934), when desiccation has proceeded some way. The comparatively restricted habitat of Blatella germanica as compared with Blatta orientalis may be further attributable in part to its higher preferred temperature, which is less easily found in this country, and in part to the fact that its females carry the egg capsule about till the young hatch; the embryos are thus exposed to the same risks as the parents, while in the other two species the capsules are safely buried.

B. orientalis adults are more easily obtained from houses during the summer and early autumn, and it seems likely that to a large extent the winter is passed in the embryonic and early nymphal stages, and the whole cycle is completed in about a year. In Periplaneta americana the duration of development is not known, but since it is the largest species it probably takes more than a year. This may lead to an explanation of its failure to establish itself in this country outside the tropical houses of Zoological and Botanical Gardens, with their lack of seasonal variation in conditions.
SUMMARY.

1. The rates of desiccation of three species of cockroaches (*Periplaneta americana*, *Blatta orientalis* and *Blatella germanica*) in dry air at various temperatures have been compared (Fig. 1). There are clear specific differences.

2. The rates of respiration of the three species are proportional to the weight to the power of 0.75–0.8.

3. In all three species, at 30° C. in dry air the animal loses about 6 mg. of water by evaporation for every 1 mg. of oxygen consumed. The smallest species (*Blatella germanica*), with the thinnest cuticle, loses least rapidly per unit surface area. These facts are consistent with the previous conclusion that the water passes through both the spiracles and the cuticle.

4. The upper limit of preferred temperature of *Periplaneta americana* and *Blatella germanica* is 33° C., while for *Blatta orientalis* it is 29° C. The lower limit is not so sharply defined and further work is required before it can be regarded as significant.

5. Certain suggestions are made concerning the ecological significance of the observations described.

I wish to thank Prof. H. Munro Fox for assistance rendered during the course of this work.

REFERENCES.


