THE TEMPERATURE AND HUMIDITY RELATIONS OF THE COCKROACH (*BLATTA ORIENTALIS*)

I. DESICCATION.

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(With Five Text-figures.)

CONTENTS.

In a series of studies, of which this is the first, I propose to bring experimental methods to bear upon the relation between a convenient insect—*Blatta orientalis*—and some of the physical factors in the environment—namely temperature and humidity. The cockroach is very susceptible to desiccation (Zabinski, 1929; Gunn, 1931), and this paper is concerned with the relation between the speed of desiccation and the dryness of the air[1] at various temperatures.

I. EXPERIMENTS ON RATE OF LOSS OF WEIGHT.

(1) *Methods.*

Each animal, during a desiccation experiment, was kept in a bottle in which the humidity was controlled, and the bottle was put into a constant temperature oven. The bottles were half-pint honey jars (200 c.c.) with tinned lids. The top edge of each bottle was ground flat and fitted with a rubber washer to prevent leakage. The

[1] The term "dryness" is here synonymous with "saturation deficiency." According to Brooks (1915–17), "by 'saturation deficiency' is meant the difference between the actual tension of aqueous vapour present in the air at the temperature in question and the tension of aqueous vapour that would be present in a saturated atmosphere at the same temperature." In stationary air, the rate of evaporation from a free water surface is closely proportional to the saturation deficiency, whatever the temperature. See also Shelford (1914) and Buxton (1931).

humidity was controlled by sulphuric acid of the appropriate concentration (Landolt-Börnstein, 1905) contained in a small tube (*ca.* 7 c.c.) suspended from a hook soldered to the lid of the jar. Electric ovens were used for temperature control.

Every effort was made to ensure that the bottles should not leak, for a considerable leakage inwards of water vapour might make the attempt at humidity control useless. It was found that liquid water did not enter when bottles were left submerged for several days, but in order to test the accuracy of the humidity and tem-

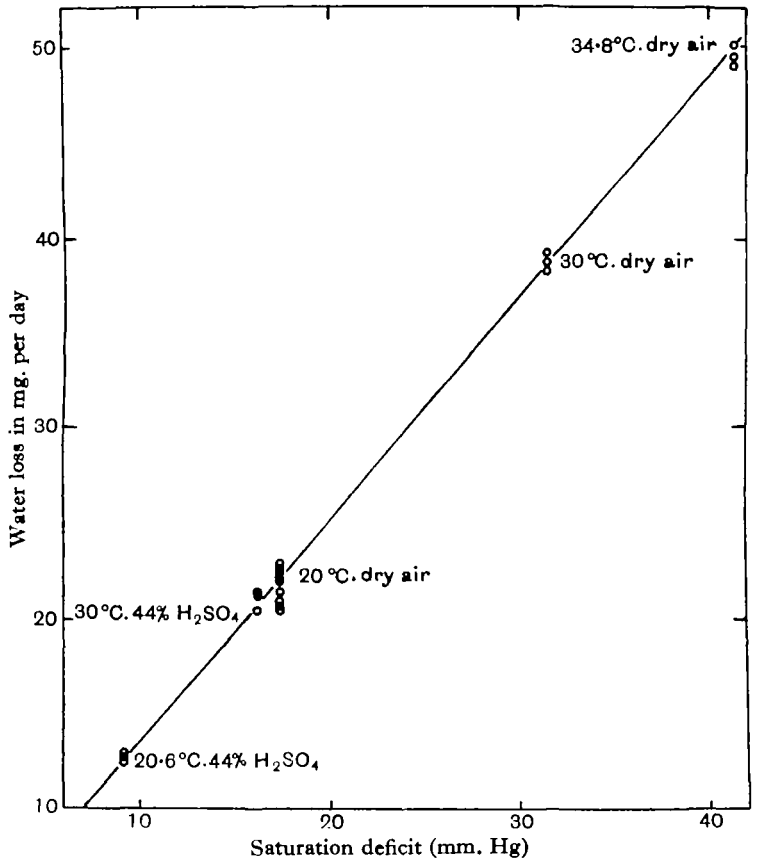

Fig. 1. Rate of evaporation of water from "artificial animals" plotted against saturation deficiency for various temperatures and humidities.

perature control fully, an "artificial animal" was made. A 7 c.c. tube was fitted with a bung and an exit tube, and lined with wet filter-paper. The length and diameter of the exit tube were adjusted until the rate of loss of water at 30° C. in dry air in the ordinary honey jar and oven was about the same as that in an average animal. Nine such "artificial animals" were kept at various temperatures and humidities under exactly the same conditions as the experimental animals, and weighed before and after desiccation (Fig. 1). When it is remembered that an error of half a milligram was possible at each weighing and that the "artificial animals" were not

absolutely identical, it will be seen that the rate of loss of water was quite nearly proportional to the dryness of the air as calculated from the temperature of the oven and the strength of acid used.

A careful consideration of all possible sources of error leads me to conclude that any single observation of rate of loss of water under the conditions of these experiments will not differ by more than about 10 per cent. from the value which would be obtained if there were no experimental errors, while the mean of a number of independent observations will be much closer to this value. As will be seen, the variation in rate of weight loss among the animals used is much greater than this.

(2) *Variation in the material.*

In the early desiccation experiments, an enormous variation in the rate of loss of weight was found. For example, at 30° C. in dry air, one animal lost 5·5 per cent. of its weight per day and lived for 8 days, while another lost 32·2 per cent. and died in 1 day. The most careful attention to the physical conditions hardly reduced the variation at all, and it was necessary to make trials of all kinds in order to obtain more consistent results. Greater consistency was certainly obtained, but the real causes of much of the variation were not discovered in the course of a very large number of experiments.

These experiments led to the conclusion that the rate of loss varied according to the place of capture of the animals and the treatment they received after capture. Accordingly, in the final experiments, animals from one source alone were used, and their treatment was carefully standardised. After capture, the adult males were separated from immature animals and females, and they alone were used, in order to avoid complications due to growth and to egg laying. They were placed in a warm room (20° C.) in uncovered glass dishes, and given nothing but sugar solution and water for 6 days. This diet was intended to reduce defaecation and to ensure that the animals were not partly desiccated before the experiment started. During the first 2 or 3 days a small proportion of the animals died, but those remaining were active and appeared healthy.

A sample of data obtained in preliminary experiments in which the animals were weighed daily is summarised in Fig. 2. From this it will be seen that out of thirty-two animals kept in dry air at 30° C., five lived for 6 days and lost an average of 46 per cent. of their original weight, while at the other extreme four animals lived for 2 days and lost about 23 per cent. At first, and also just before death, the rate of loss was higher than during the rest of the period.

The question that arises is how a representative rate of loss of weight is to be arrived at from such data. It is immediately obvious that an experiment with one animal is of no value at all, for the long-lived cases in Fig. 2 lost *on an average* about 7½ per cent. per day, the short-lived ones lost 11½ per cent. per day, while single individuals showed an even greater range of variation. Further, the rate of loss by a single individual varies from day to day, and since at 20° C. life lasts a fortnight to 3 weeks, and at 36° C. only a day, it would not be admissible to desiccate for a period shorter than the shortest life and to derive therefrom a rate of loss.

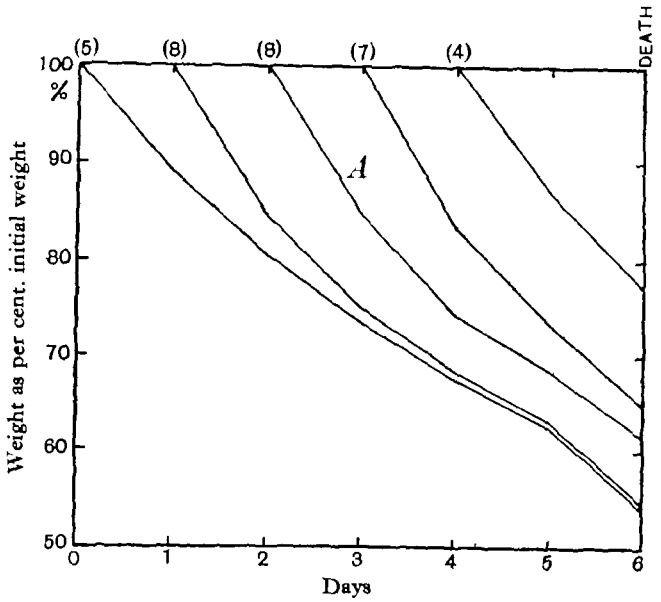

Fig. 2. Variation in the material. The weight of adult male *Blatta orientalis* (thirty-two cases) is plotted against time. They were kept in dry air at 30° C., and weighed each day until death. The figures in brackets indicate the number of animals represented by each curve.

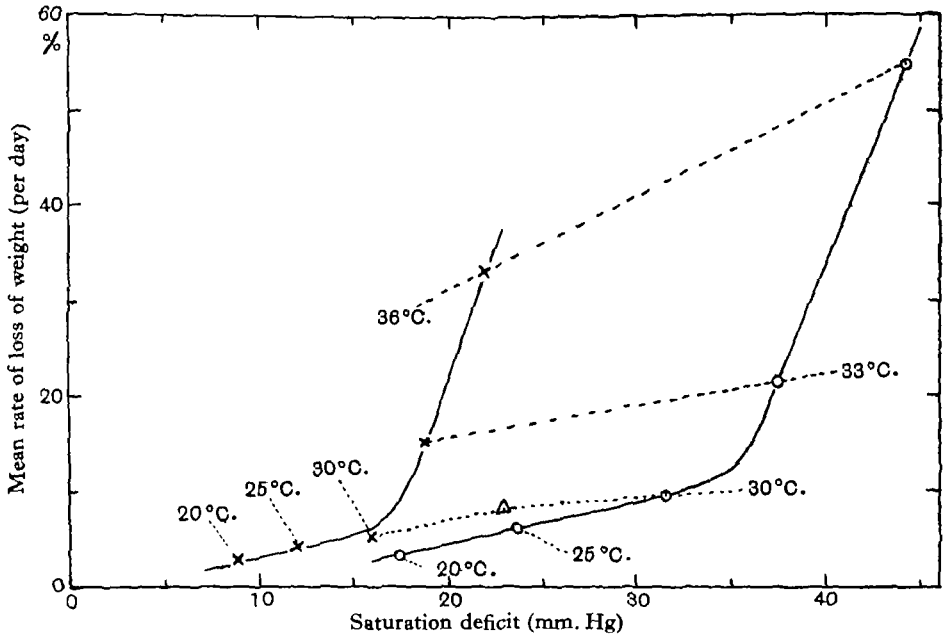

Fig. 3. Rate of loss of weight plotted against the dryness of the air. Each point represents a mean value obtained from not less than ten animals. ⊙ = conc. H_2SO_4, dry air. △ = 55·5 per cent. H_2SO_4, relative humidity = 26 per cent. approx. × = 43·75 per cent. H_2SO_4, relative humidity = 50 per cent. approx.

(3) *Experimental results.*

The procedure adopted finally was as follows. Each animal was desiccated to death and then weighed. The rate of loss of weight was calculated for each individual and the average for not less than ten animals was found. Experiments on these lines were carried out at temperatures from 20 to 40° C., in dry and in approximately half-saturated air. The average initial weight of the 142 animals used in the final series of experiments was 380 mg., the total loss of weight was 42 per cent. and the percentage of water left in the body at death was 61 per cent. The results are shown in Fig. 3. The results of experiments at 40° C. are not included, for at this temperature only about 20 per cent. of the original weight was lost before death, and death was therefore probably due to heat stroke (Mellanby, 1931).

It is clear that the rate of loss is not proportional to the dryness of the air, for the points fall on two distinct lines, neither of which is straight.

II. EXPERIMENTS ON THE RATE OF RESPIRATION.

Changes of weight in a desiccating cockroach may be due to gain of oxygen and loss of carbon dioxide as well as to loss of water. In order to assess these changes determinations of rate of oxygen intake were made by means of the Barcroft apparatus. The insects used were again adult males alone, but in this case they had been bred in the laboratory. In order to control the humidity, a carpet of wet filter-paper was fitted to the bottles. This is essential, for if defaecation takes place during an experiment, the readings are spoiled by the rise in pressure due to evaporation of water from the faeces. For the lower temperatures, Brodie's solution (Péterfi, 1928) was used as the manometer fluid, and for the higher temperatures, mercury. It was thus possible to make prolonged experiments at all temperatures. The temperature of the thermostat was more constant than was necessary (± 1/20° C.). Each animal was taken over the whole temperature range from 20 to 36° C. twice, first up and then down, or *vice versa*, a day being spent on measuring the oxygen consumption at each temperature. The animals were returned to their constant temperature oven each night and fed with carrot. The results are shown in Fig. 4.

As explained above, the respiratory rate of each animal was measured twice at each temperature, and there was usually a difference between the two rates so observed. In four cases out of the twenty-five, the divergence amounted to 40 per cent. of the lower value, but in all other cases the correspondence was much closer. In addition to erratic variations of this kind—partly due to differences in activity—there were fairly constant differences between the individuals used. For example, one animal had a low rate of respiration which was about 30 per cent. below the average for the whole five for all temperatures.

In Fig. 4, the average rate of oxygen intake is plotted against the temperature, and it will be seen that the curve is fairly smooth. The acceleration in respiration with rising temperature is due to increased activity as well as to rising basal metabolism. No attempt has been made to measure carbon dioxide output, but with the

aid of these data for oxygen, it is possible to estimate the order of magnitude of losses of weight other than water.

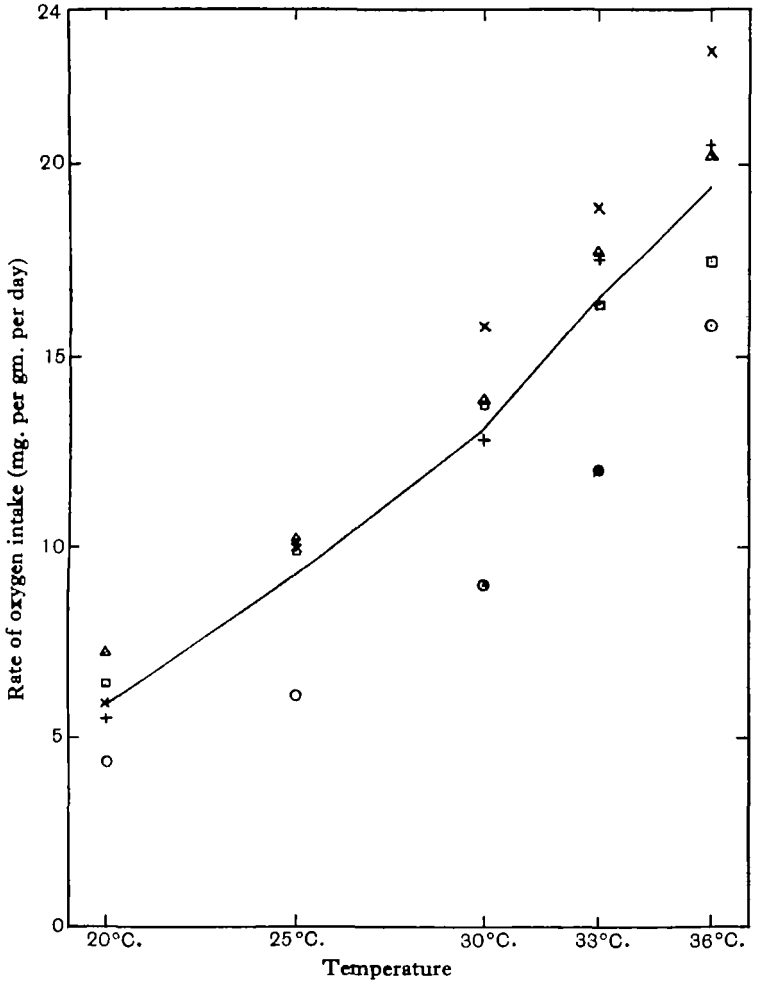

Fig. 4. Rate of consumption of oxygen of five animals, each of which is represented by a characteristic symbol. Each point represents the average steady rate from two or three experiments, each lasting a day. The curve shows the mean rate for the five animals.

III. RATE OF LOSS OF WATER.

If a cockroach is neither fed nor allowed to drink, the only cause of increase of weight is the oxygen taken in, and the only causes of decrease in weight are losses of water vapour, carbon dioxide, and faeces. These facts may be represented by the equation

$$W_1 + aO_2 = W_2 + bCO_2 + cH_2O + \text{faeces} \quad \text{.....(i),}$$

where W_1 and W_2 are the weights of the animal before and after a certain time has elapsed, and a, b, c represent the weights of the gases taken in or given out during

that time. Remembering that the respiratory quotient (R.Q.), is expressed in terms of volumes, equation (ii) is easily derivable from equation (i):

$$W_1 - W_2 = aO_2 (\tfrac{11}{8} \text{ R.Q.} - 1) + cH_2O + \text{faeces} \qquad \text{.....(ii).}$$

From this equation, it will be seen that if the respiratory quotient is exactly 8/11 or 0·73, there is no change in weight due to respiration. If it is less than this, gain due to intake of oxygen will be greater than the loss due to carbon dioxide. According to Davis and Slater (1926) and Slater (1927) the respiratory quotient in this cockroach lies between 0·72 and 1·0 and tends to fall to the lower value during starvation. The loss of weight due to respiration will therefore lie between zero and 3/8 of the weight of oxygen taken in, with a tendency to fall to zero. For 20° C. the intake of oxygen amounts to about 6 mg. per gm. per day, so that the resultant weight loss directly due to respiration will be not more than 2 mg. per gm. per day, while for 30 and 36° C. the values are approximately 5 and 7 mg. For these three temperatures, the mean total loss of weight from all causes in half saturated air is 23, 52, and 328 mg. per gm. per day (Fig. 3), so that changes in weight due to respiration have an upper limit of 10 per cent. of the total.

The only remaining source of loss is defaecation. In a desiccation experiment the faeces lose water before it is possible to weigh them, so no exact measure can easily be made of this source of error. But the *total* quantity of faeces deposited had an average weight (partly dried) of only about 4 mg. (1 per cent. of the animal's initial weight). Certainly a precise investigation of losses due to faeces would not bring the points on Fig. 3 on to two straight lines, far less on to one.

When the gross rates of loss of weight, corrected by the maximum deductions for loss of carbon dioxide and a small deduction for faeces, were plotted against the dryness of the air, the graph differed very little from Fig. 3. It can therefore be said that in *Blatta orientalis* the rate of water loss is not simply proportional to the dryness of the air, and in order to find a simple correlation it is necessary to go more deeply into the matter.

IV. CORRELATION OF SPEED OF DESICCATION AND EXTERNAL CONDITIONS.

(1) *A new formula.*

It we neglect the anus and the mouth, water may be lost by two channels, the spiracles, and the general body surface. Provided that there is no absolute upper limit to the rate at which water may pass through the cuticle, this loss would be proportional to the dryness of the air.

Only the spiracles remain to be considered. It has been held that spiracular closure is a mechanism which prevents water loss (Hazelhoff, 1927). At least it is certain that some water vapour must escape while oxygen is entering the respiratory system. The work of Hazelhoff shows that normally, when diffusion alone is regulating the supply of oxygen to the tissues, the valves open only when the carbon dioxide pressure just inside the spiracle reaches a certain value (2–3 per cent.).

(Ventilation regulation—accompanied by pumping movements—sets in at a much higher tension of carbon dioxide.) Moreover, the spiracles are more widely open—and open for longer periods—when the animal is active, or when the temperature is higher, than when the animal is quiet, or the temperature is low. If it were possible to measure the time for which spiracles opened and the extent to which they opened, and to give a result in say square millimetre-hours, this figure would probably be proportional to the total respiration during the same period. That is, the rate of respiration may be used as a measure of the degree and duration of spiracular opening. Further, the amount of water lost through the spiracles under the same conditions (diffusion regulation) will be proportional to the same quantity —*i.e.* the degree and extent of opening—and therefore to the rate of respiration. If the air in the trachea is saturated and that outside is not, the rate of water loss will also be proportional to the dryness of the outside air. Consequently the rate of loss of water through the spiracles alone should be proportional to the product of the rate of respiration and the dryness of the outside air. The total loss of water from spiracles and body surface may then be represented by the equation

$$\text{Rate of loss} = kdo + k'd \qquad \text{.....(iii),}$$

where k and k' are constants for animals of the same structure, d is the dryness of the air, and o is the rate of respiration. If this equation truly represents the state of affairs, and if the right values of k and k' are obtained, rate of loss plotted against $kdo + k'd$ should give a straight line.

One limiting case, when k is assumed to be zero, has been illustrated in Fig. 3, where rate of loss is plotted against dryness of the air, and the points do not fall on a straight line. The other limiting case, when k' is assumed to be zero, is shown in Fig. 5. It is clear that from 20 to 30° C. there is a tolerable approximation to a straight line, but above 30° C. the formula certainly does not fit the facts (see section iv, part (3)).

It has already been seen that a closer approximation to a straight line is given by $k' = 0$ than by $k = 0$ (Figs. 5 and 3), that is to say, there is at least some water lost through the spiracles, but so far there is no indication of the amount of water lost through the surface ($k \neq 0$, but k' may $= 0$). If any arbitrary value is given to k, and a series of values from zero upwards given to k' in turn, a series of values can be calculated for $kdo + k'd$ for each set of conditions. The experimental data are not sufficiently consistent to show exactly what values of the two constants fit best, but it is very probable that at 30° C. up to 30 per cent. of the water loss may take place from the body surface. In this case, at 20° C., surface loss will be not more than 50 per cent. of the whole (cf. Green, 1932).

(2) *Consideration of the assumptions involved.*

The principal assumption made is that the respiratory rates, obtained from well-fed animals by means of the Barcroft apparatus with saturated air, are indeed a measure of the amount by which the spiracles are opened in the desiccation experiments. Now in this connection the importance of these Barcroft experiments is not

that they give an exact measure of the oxygen intake, but that they give a temperature coefficient of respiration. If the respiratory quotient changed with temperature, the rate of oxygen intake would not be a measure of spiracular opening at different temperatures. Since, however, there is no reliable evidence to show that the respiratory quotient does change in this way, it can be assumed here that it does not. Experiments have been started in order to find out what effect is produced by dry air and by desiccation on oxygen intake and on carbon dioxide production at various temperatures.

The only other important assumption is that the air in the tracheae is saturated at the temperature of the environment. The insect trachea is very permeable to gases

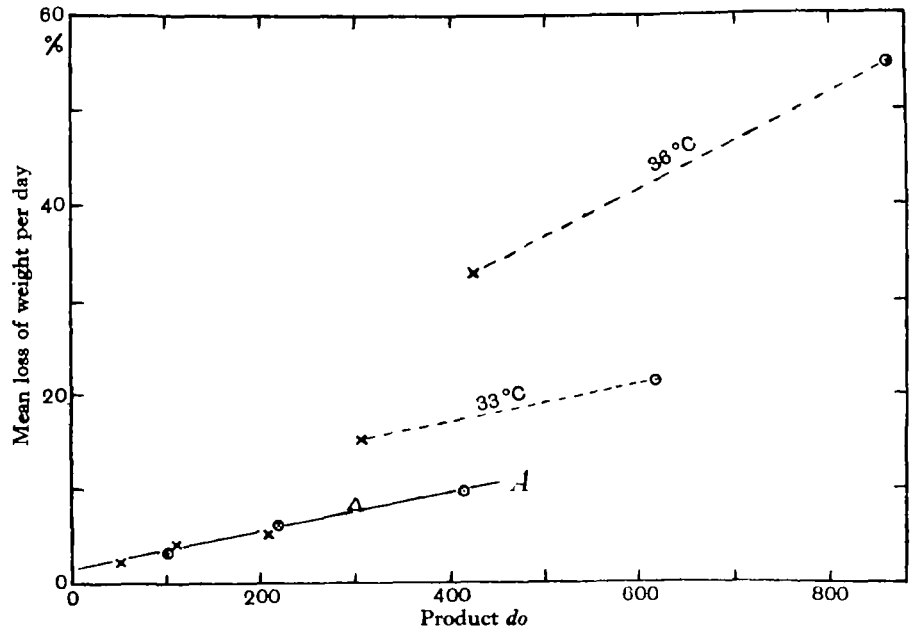

Fig. 5. Rate of loss of weight plotted against the product of dryness of the air and rate of oxygen consumption. For explanation of symbols see Fig. 3, which is based on the same desiccation experiments. The points fall on a straight line for temperatures from 20 to 30° C. only (Curve *A*).

(Wigglesworth, 1930, 1931), and it can hardly be doubted that water vapour would penetrate from the blood and tissues sufficiently quickly to saturate the air at the temperature of the animal, and the body temperature is not appreciably different from that of the environment up to 30° C. (Necheles, 1924; Bodenheimer and Samburski, 1930).

If, then, we come to the conclusion that a large part of the water lost by the cockroach passes through the spiracles rather than through the body surface, there is a ready—but only partial—explanation of the great variation in the rate of this loss. It has been shown above that there are constant differences between the respiratory rates of individuals, and also variations due to changes in activity. One animal may use twice as much oxygen as another in a given time, with a consequent

proportionate difference in water loss. So that we need look no further to find causes for the variation in water loss, unless it be to find causes of variation in resting metabolism and in activity.

(3) *Divergence from the formula above* 30° C.

But when we come to consider the divergence from expectation above 30° C., the case is rather different. The greatly increased rate of loss might be attributed to rapid accumulation of carbon dioxide in the bottle causing increased spiracular opening. An experiment was carried out (36° C., R.H. = 50 per cent. approx.) in which the carbon dioxide was absorbed by caustic soda of the appropriate concentration, but the rate of loss was not diminished.

According to Hazelhoff, at 33° C. the spiracles of the cockroach *Periplaneta americana* remain constantly wide open. If, as seems probable, this is ultimately an adaptation which ensures a sufficient oxygen supply, somewhere in the temperature region between 30 and 33° C. there must be a critical point at which diffusion through constantly open spiracles can just maintain the required concentration of oxygen in the tracheoles (or, more exactly, can just prevent the carbon dioxide from rising above the concentration required to open the spiracles). If this temperature is exceeded the spiracles cannot open more widely, but the oxygen consumption and carbon dioxide production will tend to increase. Oxygen consumption will then cease to be a measure of the degree of opening of the spiracles, and the equation (iii) cannot be expected to hold. Further, when this critical temperature is exceeded, pumping movements of the abdomen—which are believed to ventilate the tracheae (Demoll, 1927)—set in even in the absence of special activity. This means that water vapour will no longer simply diffuse out of the tracheal system, but it will be actively swept out. Since the point in the tracheal system across which there is diffusion but no flow is now transferred from the spiracles to within the body, so that it lies between the points where water vapour can be lost (the main tracheae) and where oxygen is absorbed (the tracheoles), the rate of water loss will certainly no longer be proportional to the oxygen intake. Any attempt to find a simple relationship between the dryness of the air and the rate of water loss when ventilation regulation is in operation must meet with the greatest difficulties of theory.

It is impossible to find experimentally a temperature at which *B. orientalis* abandons diffusion ventilation for ventilation regulation. Even below 30° C., pumping movements do occur during and after great activity. But at about 32° C. in most individuals they never cease, and as the temperature rises further they become more and more frequent. This explains why at 33° C. the water loss is 140–200 per cent. of the value calculated from equation (iii), while at 36° C. it is 270–320 per cent. of this expected value. Further, it may provide a partial explanation of the variation at lower temperatures, for greater activity will produce a disproportionately greater loss of water if pumping movements take place.

V. CONCLUSIONS.

It seems therefore that the size of the tracheal system sets the limit to the amount of oxygen which can be obtained by diffusion, and that between 30 and 33° C. diffusion regulation fails in the cockroach and ventilation regulation sets in as a normal process, involving greatly increased losses of water. At about 30° C. therefore there is a crucial temperature, fixed by the dimensions of the tracheal system, at which the rate of loss of water increases out of all proportion to the gain of oxygen, and, in effect, the water conservation mechanism of the respiratory system fails. If the air is dry and if supplies of water for drinking are not available, a cockroach kept at a temperature higher than this must speedily die. Here then is an upper limit to the temperature range of *Blatta orientalis*, fixed by the speed of desiccation. At 40° C., the animal dies in about 4 hours whatever the humidity, so that in saturated air heat stroke fixes the upper limit of temperature at 36–40° C., while for dry air desiccation fixes it at a little above 30° C.

In similar experiments on the same species, Necheles has obtained results which differ radically in matters of fact from mine. He finds, for example, that the rate of water loss in dry air does not increase much when the temperature is raised from 35 to 40° C., whereas for dry air my figures for 33, 36 and 40° C. are 21, 55 and 160 per cent. of the original weight lost per day. He says that at about 33° C. irreparable damage is done by heat, whereas I find in respiration experiments in saturated air that after being kept at 33 and 36° C. for 2 days each, the respiratory rates of the animals at lower temperatures are not markedly changed. He concludes that above 30° C. body temperature is kept below that of the environment by a special additional loss of water vapour, and that there is an elementary kind of temperature control by this means, resulting in the toleration of higher environmental temperatures than would otherwise be possible. On the contrary, I would say that the rate at which water is lost in dry air at these temperatures is definitely harmful, while the temperature alone is not so, as shown by its effect in combination with saturated air. The additional water loss occurs in virtue of a weakness of the respiratory system and is not, as Necheles would have it, a definite advantage when high temperatures are met with.

Buxton (1930) has been carrying out experiments parallel to mine, using the larva of *Tenebrio molitor* (mealworms). He has met with great difficulties due to variability of material. Apart from the results from three batches in drier air at 23° C., for which he erects a special theory, his figures and those of Mellanby (1932) are not inconsistent with my formula, for at one dryness the rate of water loss rises with the temperature.

VI. SUMMARY.

1. The rate of loss of weight of adult male *Blatta orientalis* was measured in half-saturated and in dry air at various temperatures from 20 to 40° C.

2. The rate of consumption of oxygen was measured in saturated air over the same temperature range.

3. If no correction is made for losses of weight other than water loss, the rate of total loss can be taken as a satisfactory measure of the rate of water loss.

4. At different temperatures the rate of water loss was not proportional to the saturation deficiency of the air. The rate of loss in dry air was proportionally too low (or the rate at higher temperatures too high) to fit this relationship.

5. A formula was found for the rate of loss at all temperatures from 20 to 30° C., and the conclusion was reached that most of the water escapes through the spiracles rather than from the body surface.

6. Above 30° C. the rate of loss is much greater, due to a change of respiratory mechanism from diffusion regulation to ventilation regulation.

7. *Blatta orientalis* dies from heat stroke at a minimum temperature between 36 and 40° C. It will die from desiccation at any of the temperatures and humidities studied, but the speed of desiccation increases very rapidly above 30° C. owing to the form and mode of action of the tracheal system. Desiccation sets an upper limit to the temperature range of the species, which is below the heat-stroke temperature.

8. The view that the temperature range of the species is increased by a regulation of body temperature through a rapid loss of water vapour is untenable.

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