THE HUMIDITY REACTIONS OF THE WOOD-LOUSE, *PORCELLIO SCABER* (LATREILLE)

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(With Five Text-figures)

I. INTRODUCTION

IN recent years a considerable amount of work has been done on the effects of air humidity on animals (Buxton, 1932, Mellanby, 1935). The reactions of animals to air humidity have been relatively little studied (Herter, 1926, 1932). Now that suitable apparatus for precise humidity behaviour studies is available (Gunn & Kennedy, 1936), considerable advances can be made. The alternative chamber designed by Mr Kennedy in this Department has been particularly useful in the present investigation. This paper contains a general account of the reactions of the wood-louse, *Porcellio scaber* (Latreille), to humidity.

P. scaber is probably inferior to no other crustacean in its success in colonizing the terrestrial environment. The principal structural adaptation to be noted is the possession of pseudotracheae in the pleopods (corpora alba) (Calman, 1909), through which most of the respiratory exchange takes place (Reinders, 1933). *Porcellio* is commonly to be found in and under rotten wood, upon which it feeds, in a microclimate which is thus characteristically damp. If it is kept in dry air at 20° C., it loses weight (largely water) at an average rate of 4 per cent of its original weight per hour, and dies in a few hours. On comparison with the desiccation rates of the mealworm (0·05 per cent per hour at 23° C. (Buxton, 1930)), the cockroach (0·14 per cent per hour at 20° C. (Gunn, 1933)), and the earthworm (*Allolobophora* sp.) (18 per cent per hour at 20° C. (unpublished observation)), this figure indicates the relatively urgent need of the wood-louse for water. It would therefore be surprising if the species had survived without some kind of reaction to keep it in damp places.

Allee (1931) described experiments in which wood-lice were kept in chambers of three kinds; in a very dry chamber, the animals were active until they died; in a fairly dry one, they formed stationary clumps; in a very moist chamber, they scattered and remained motionless. Wolsky (1933) found that when given a choice, *Porcellio scaber* settled on moist cotton wool but not on dry, and the behaviour of the animals justified him in describing the reaction as a hydrokinesis. In the experiments to be described, the animal is not allowed to touch liquid water at all, and the reactions which are investigated are reactions to air humidity. The prefix *hygro-* is therefore appropriate, instead of *hydro-*, in naming these reactions.

The apparatus used for these experiments has been described in principle (Gunn, 1934; Gunn & Kennedy, 1936), and only slight modifications and variations need be mentioned here.

II. GENERAL HUMIDITY BEHAVIOUR

The first apparatus used was the straight gradient apparatus, 2·5 m. long, (*A* 1[1]), in which the humidity is accurately known at all points. A number of wood-lice put into this collect at the moist end within an hour or two. No variation of reaction is observed when the drying agent is changed from concentrated sulphuric acid to phosphorus pentoxide or granular calcium chloride. Transport of water vapour along the gradient is very slow, so that there is no measurable difference of temperature between the two ends due to evaporation and condensation, and the stimulus to aggregation at the moist end is therefore not provided by temperature differences. Indeed, it has been found that in the temperature gradient apparatus (Gunn, 1934) *P. scaber* goes to the moist place wherever that may be in the temperature gradient. If there is indeed a preferred temperature, the humidity preference is so strong as to hide it. It is therefore possible to use the much handier alternative chamber (*A* 2) in which the drier side may be 1·5° C. warmer than the moister side.

The glass chamber here used was 22 cm. in diameter, and 4·5–5 cm. high. The two halves of the floor were covered with Petri dishes containing concentrated sulphuric acid on one half and distilled water on the other, in such a way that the two sets of dishes were contiguous along a diameter of the chamber, the boundary. Within a few minutes of being placed in this apparatus, all the wood-lice collected into the moist side. Later, at any one moment about three-quarters of them were quite still, and the rest were moving about, poking their antennae through the holes in the perforated zinc platform, or performing cleaning movements. At intervals a wandering individual would go towards the dry side of the chamber. Either of two things would then happen; the animal might walk smoothly into the dry region, or it might show some sort of deviation or hesitation. In the former case there was very frequently an acceleration of pace in the dry region, and the animal practically never came to rest there. Consequently, it quickly re-entered the moist side of the chamber, where it sooner of later came to rest. This is a perfectly clear case of hygrokinesis (Kühn, 1919; Savory, 1930; Wolsky, 1933), and is in itself a sufficient mechanism for such a humidity preference. There is in the wood-louse, however, a further mechanism of a more economical kind. In its most complete form, this further reaction is an ideal avoiding reaction like that shown by *Paramecium* (Jennings, 1906). On approaching the humidity boundary, the animal stops suddenly,

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[1] The index number refers to the type of apparatus as already described (Gunn & Kennedy, 1936).

rarely even swaying back slightly, pivots about its centre, and walks off in a new direction. Sometimes, in addition to turning before starting to move off, the animal subsequently follows a curved path, so that it immediately goes back into the moist air. At other times the avoiding reaction is ineffective, so that in spite of the change of direction the animal goes into the dry region. In the Kühn nomenclature (Fraenkel, 1931), *Porcellio scaber* therefore shows hygrophobotactic behaviour.

The reaction described above does not occur only at the humidity boundary, or region of most rapid change of humidity, but also at other points on both sides of the chamber, where the humidity gradient is less steep. Further work on this reaction is projected, particularly in the light of the results of Ullyott (1936) for *Dendrocoelum lacteum*.

This behaviour of wood-lice is very easily demonstrated and has been found to be a good subject for class experiments.

III. LIMITS OF REACTION

In order to find the lower limit of humidity difference to which the animals react, and to measure the degree of reaction with various humidity differences, the alternative chamber was used in the following way. Sulphuric acid and water mixtures of appropriate concentrations (Landolt-Börnstein, 1905) were put into dishes 7·5 cm. in diameter and 2 cm. deep, two dishes on each side of the chamber. A hygrometer was put on the perforated zinc platform on each side with the pillar which supports the sensitive paper 3 cm. from the edge of the chamber. It is the difference of humidity between these two pillars, 16 cm. apart, which is recorded below, and, since the apparatus was otherwise invariable, this difference is sufficient to characterize the gradient used in any one experiment. Nevertheless it must be remembered that the humidity varies from point to point across the chamber. A sample gradient is shown in Fig. 1, obtained from acids in equilibrium with air at 39 and 67 per cent R.H. (relative humidity) respectively.

In each experiment the apparatus was set up in the evening. On the following morning five animals were put into the chamber through a small central hole in the glass lid, and at intervals of about 15 min. their positions were recorded. Any animals which were motionless were so recorded, and individuals within 1·5 cm. of the boundary were put into a separate category. After the reading, the animals were stirred up by means of a pipe-cleaner pushed through the hole in the lid, so that no animals remained motionless, and so that after stirring there were either two animals on each side and one in the middle, or three animals on the side which had previously had the smaller number and two on the other.[1] At the end of the day (twenty readings, giving 100 position records) the animals were taken out and returned to the culture. The sulphuric acid dishes were interchanged, while the perforated zinc platform, the lid and the hygrometers were kept in the same position relative to the chamber. On the following day, twenty more readings were taken. In this way the

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[1] It is believed that the abnormality of position of the point *A* in Fig. 3 is due to laxity in following these rules.

effects of any attractive or repellent features of the apparatus were cancelled out, so that in the aggregate the animals could only be reacting to the dishes of sulphuric acid. Factors external to the chamber were controlled by rotating the chamber through 180° half-way through each day's work. Each experiment was further accompanied by

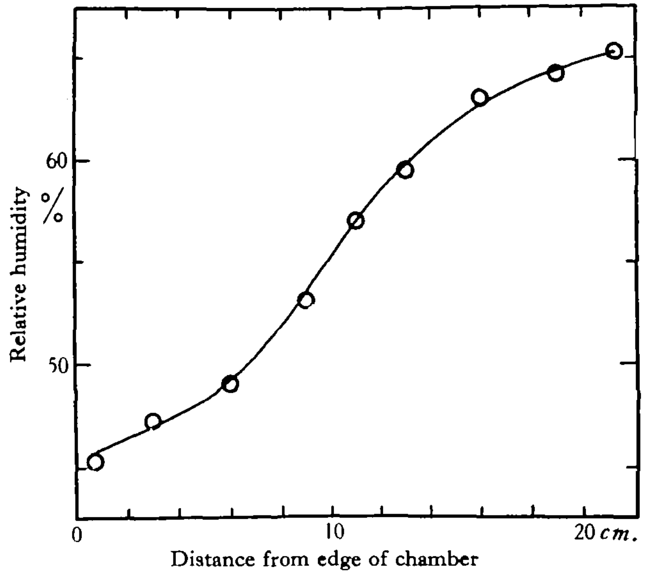


Fig. 1. Humidity gradient, such as was used in the experiments on the limits of reaction.

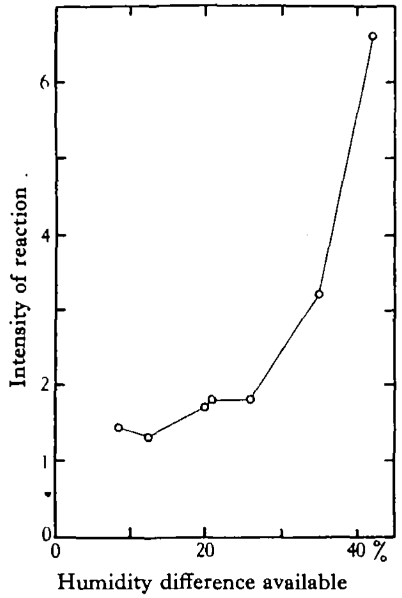


Fig. 2. Relation between humidity difference available and intensity of reaction. The lower humidity was always the lowest obtainable with concentrated sulphuric acid. The intensity of reaction here means the number of records of animals on the moister side divided by the number on the drier side.

a control identical in all respects, except that the humidity was constant throughout the chamber. The chambers were kept near a north window, and shielded from direct light. The temperature was fairly constant during any one day, and varied from 15 to 20° C. during the whole series. The humidity difference was recorded by *each* hygrometer, for each was first over one strength of acid and then over the other. Measurements taken in this way proved to be consistent and reliable for even small differences.

The results of these experiments are recorded in Figs. 2 and 3. The intensity of reaction is conveniently measured by the number of records of animals in the moister side divided by the number in the drier side, those in the middle (av. 13 per cent of all the records, maximum, 22 per cent) being omitted. In the controls, the limits of this "intensity of reaction" in thirty-five experiments were 0·60–1·55 (av. 1·001 ± 0·04), the humidity being uniform. In Fig. 3 the controls are represented by black circles and the experiments by rings. For convenience, each ring is plotted on the central humidity of the range available; for example, the point *A* represents an experiment in which the extremes were 48·5 and 79·5 per cent R.H., the central humidity being therefore 64 per cent R.H., and the range available 31 per cent R.H., and there were 2·4 times as many records for the wetter side as there were for the drier. The ordinate is therefore 2·4 (times) and the abscissa 64 (per cent R.H.). Each ring above the horizontal line at intensity 1·7 represents a significant reaction. Free-hand lines have been drawn to separate points for experiments where

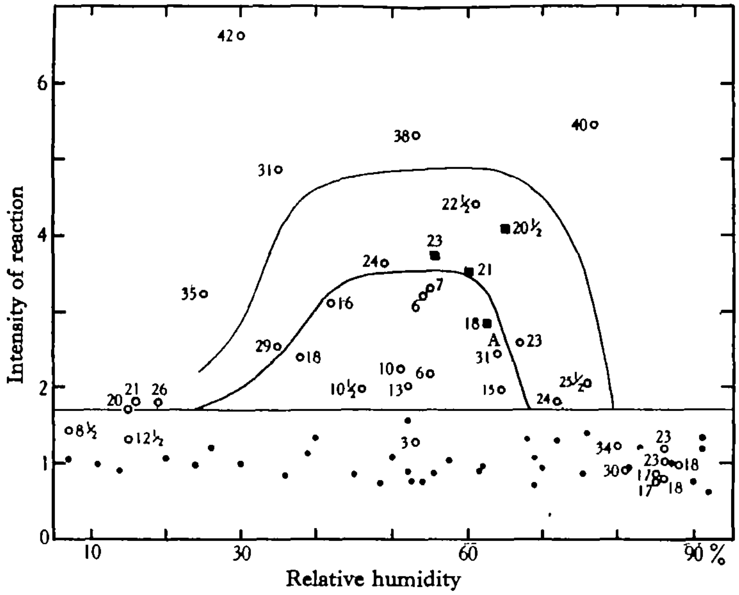


Fig. 3. Limits of reaction of *Porcellio scaber*. The point *A* shows that at 64 per cent R.H. there were 2·4 times as many records of animals in the moister side as there were in the drier, the humidity difference shown by the hygrometers being 31 per cent R.H. The two humidities were thus 48·5 and 79·5 per cent R.H. Further explanation in the text, pp. 182–183.

the humidity difference was 20–29 per cent R.H. from the other cases, where there were smaller or greater differences available to the animals.

It will be seen that the reaction was greatest between 35 and 65 per cent R.H. approximately, and that at 55 per cent R.H. there was a definite reaction to a difference of 6 per cent R.H. In the drier region the reaction diminished, so that a difference of 20 per cent R.H. was required at 15 per cent R.H., while in moister air it disappeared completely at 80 per cent R.H. There was thus no reaction to a difference of 30 per cent R.H. at 81 per cent R.H. (i.e. 66–96 per cent R.H.). Generally speaking there was no reaction in the moist region unless the lower humidity was below 65 per cent R.H. In the drier region the reaction fell off more gradually, but a reaction of intensity over 2 required an upper humidity of 35 per cent R.H. or more, while no reaction occurred if the upper humidity was below 25 per cent R.H. An examination of the data shows that, apart from a few experiments in which the humidity difference was fairly high, the excess of animals in the moister side was largely due to an excess of motionless individuals.

So far, there has been nothing to show that the reaction is really a response to humidity rather than to other chemical stimulation from the humidity controlling fluid. Stronger acid might be expected to have a stronger smell than weak acid, as well as producing a lower humidity. It is in any case clear that such chemicals do not have a universally repellent effect; for locusts (Kennedy, 1937) and certain other insects (unpublished observations) prefer dry air. Although I could detect no smell from the acid, it was necessary to control this. Four experiments were done in the middle humidity region and with about 20 per cent R.H. difference available. In the first, solutions of phosphorus pentoxide controlled the humidity; in the second, solutions of caustic potash; in the third, there was phosphorus pentoxide solution on the drier side and sulphuric acid on the wetter; and in the fourth, caustic potash and phosphorus pentoxide respectively. The results, shown as black squares in Fig. 3, are perfectly consistent with those obtained from experiments with sulphuric acid as the controlling fluid. In these experiments all of these substances have in common their water vapour pressures; it is so unlikely that they produce other chemical stimulation leading to reactions of such similar *intensities* that it is safe to say that these reactions are really responses to humidity.

Before the strictly controlled experiments were started, twelve tests were done with 2–3 per cent R.H. difference in about half-saturated air, four of them using magnesium chloride solutions. In all of these except one the wood-lice reacted positively to the moister air, though often with low intensity only. If these experiments are valid, the preference for 52·5 per cent R.H. when contrasted with 50 per cent R.H. shows that the animals are sensible of a difference of 2·5 per cent R.H.

IV. THE KINESIS

In the above experiments, the number of animals which were motionless at each reading was recorded. Fig. 4 is derived from the controls, which were done at constant humidity. The line on the graph represents the average of the points, grouped in classes of 10 per cent R.H. It shows that as the humidity rises, the proportion of motionless animals also rises. The variation in temperature during the series of experiments prevents very precise conclusions being drawn from this figure. The figure does, however, explain the aggregation of animals into the moister side of the alternative chamber, but it explains neither the absence of reaction at high humidities nor the other variations in intensity of reaction. If only experiments in which the temperature was 16–18° C. are taken into account, the curve shown in Fig. 4 becomes sigmoid, with flattened regions below 30 and above 70 per cent R.H. approximately. If, with carefully controlled temperature, this represents the real state of affairs, then it means that the constancy of activity levels in the regions 0–30 and 70–100 per cent R.H. is the immediate cause of the reduction of preference in the alternative chamber in these regions, and the other variations are explicable on the same basis.

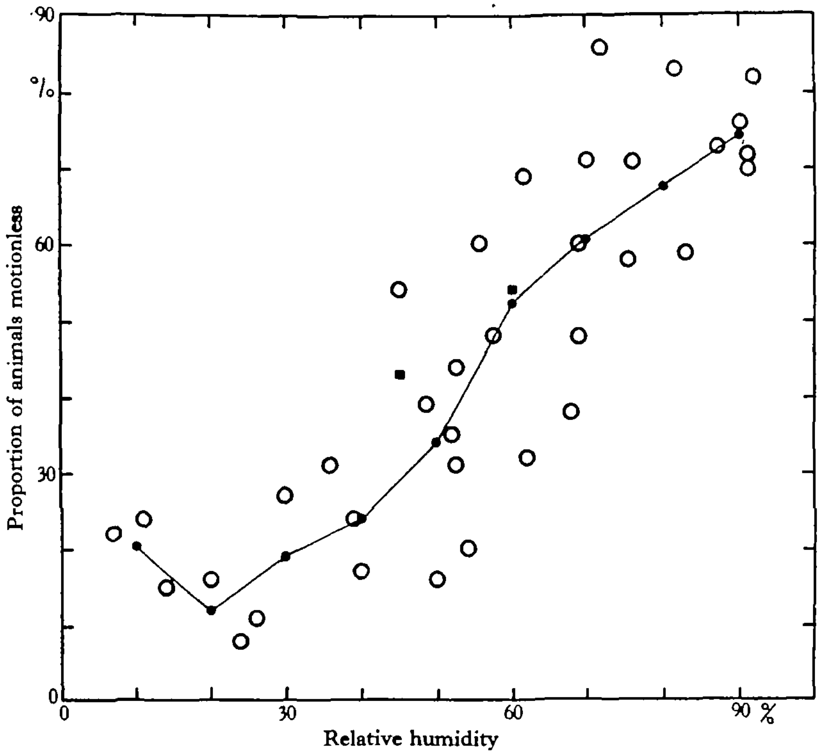
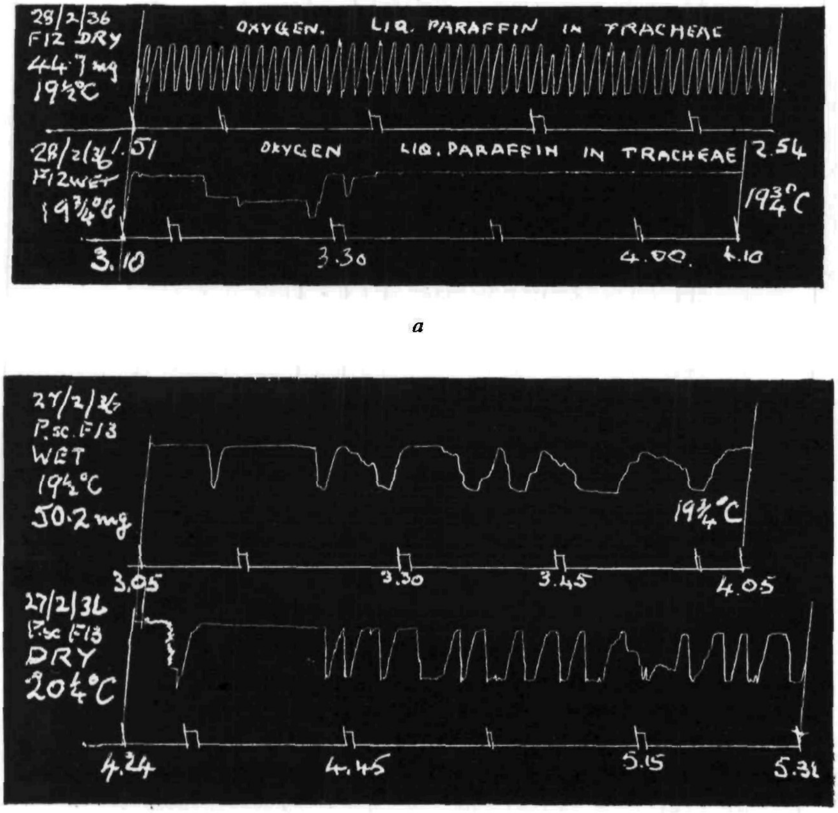


Fig. 4. Inactivity and humidity. Each point records the proportion of individuals quite motionless during a set of observations each lasting 30 sec. and 15 min. apart, at the given constant humidity. The humidity was controlled by sulphuric acid solutions except in two cases (black squares) when phosphorus pentoxide and caustic potash were used.

V. HUMIDITY RECEPTORS

The experiments with the alternative chamber described above indicate that there are in *Porcellio scaber* receptors for the humidity stimulus; for there is frequently an immediate effect on behaviour when the animal passes from wet air to dry, and the change in behaviour is quickly reversible and repeatable in one individual. The aktograph (B 1, Gunn & Kennedy, 1936) was used in the attempt to locate such receptors. It was first established that this apparatus was appropriate for the purpose. Fig. 5 indicates the results from the two main types of individuals. The first type (Fig. 5*a*) showed great and constant activity until death, when kept in air dried by calcium chloride, and very little activity in nearly saturated air; the second type (Fig. 5*b*) showed greater activity in dry air than in moist, without such a striking difference. In twenty-six individuals there were thirteen of the first type, ten of the second, and three which showed either a slightly reversed reaction or none at all. Only specimens of the first type were used in the receptor tests. After a preliminary test, the attempt was made to inactivate for humidity reception a certain part of the body, and the test was then repeated. The following eliminations were carried out: (*a*) the antennae were cut off, (*b*) the mouth parts thickly smeared with vaseline, (*c*) the pseudotracheae filled with medicinal paraffin and the animal kept



a

b

Fig. 5. Aktograph records. Each vertical line represents a journey of 6–9 in. The time intervals marked are quarters of an hour. In one individual here represented (*a*) there was much greater activity in dry air than in wet; in the other (*b*) the difference was slight.

alive and active by means of additional oxygen, (*d*) the hinder pleopods vaselined, and (*e*) the uropods pulled out. In each case the kinetic reaction remained. It seems probable, therefore, that the receptors lie in the thoracic region. This part can hardly be tested without interfering with locomotion, and further attempts will be made with a larger species. Humidity receptors have been identified both anatomically and experimentally on the legs of spiders by Blumenthal (1935).

VI. SUMMARY

1. *Porcellio scaber* exhibits hygrokinesis, being very active in dry air and almost motionless in nearly saturated air. With rising humidity a steadily increasing proportion of a batch of specimens is found to be inactive at any one moment.

2. *P. scaber* also shows hygrophobotactic behaviour.

3. The effect of both reactions is to collect the animals into moist air.

4. In a humidity gradient of given steepness the intensity of the humidity preference varies at different parts of the humidity range. There is no reaction at all if the gradient does not include a region below 65 per cent R.H. There is definite reaction to a difference of 6 per cent R.H. in approximately half-saturated air.

5. The humidity receptors, if they are confined to one area, apparently do not lie on the abdomen or on the head region.

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REFERENCES

). *Animal Aggregations*. Chicago.
935) *Z. Morph. Ökol. Tiere*, **29**, 667–719.
o). *Proc. roy. Soc.* B, **106**, 560–77.
. *Rev.* **7**, 275–320.
09). *Lankester's Treatise on Zoology*, **7**, *Crustacea*. London.
). *Biol. Rev.* **6**, 36–87.
). *J. exp. Biol.* **10**, 274–85.
ergl. Physiol. **20**, 617–25.
NNEDY, J. S. (1936). *J. exp. Biol.* **13**, 450–9.
Handb. norm. path. Physiol. **11**, 179–80.
db. norm. path. Physiol. **18**, 282.
06). *Behaviour of the Lower Organisms*. New York.
37). *J. exp. Biol.* **14**, 187.
Die Orientierung der Tiere im Raum. Jena.
N (1905). *Physikalisch-Chemische Tabellen*. Berlin.
5). *Biol. Rev.* **10**, 317–33.
33). *Z. vergl. Physiol.* **20**, 291–8.
o). *J. Ecol.* **18**, 384–5.
ULLYOTT, P. (1936). *J. exp. Biol.* **13**, 265–78.
WOLSKY, A. (1933). *Állatt. Közlem.* **30**, 26–35.