THE ABSORPTION OF WATER BY WOODLICE

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(*Received 2 January* 1954)

INTRODUCTION

Woodlice lose water rather rapidly by transpiration into unsaturated air (Edney, 1951). In nature, some loss of water is bound to occur in this way, for they are not always exposed to saturated air, and the present paper reports the results of an investigation into the means available for replenishing such lost water.

It is clear that woodlice absorb water when eating moist food, but partially desiccated animals, left in the presence of potato dice, regain their original weight even when the food is uneaten. It is not clear, in these circumstances, whether water is absorbed from the moist surface of the food (and if so by what route), or from the moist air close to the surface.

Partially desiccated woodlice can also be observed to take up water from droplets or from wet filter-paper by immersion of either the mouthparts or the terminal appendages (uropods). Some of this water at least flows along the capillary channels on the ventral surface which form the *Wasserleitungssystem* first described by Verhoeff (1917, 1920). Whether any of this water enters the alimentary canal has been an open question.

The problems are: (i) can woodlice absorb water vapour from moist air (as some insects do); (ii) do they imbibe liquid water and/or absorb water from damp surfaces, and if so, how?

Four species, chosen to cover as far as possible the range of terrestrial habitats of the group, were used for this investigation. They were *Ligia oceanica* (a littoral species), *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*. The last three are generally thought of as occurring in progressively drier habitats.

EXPERIMENTS

(*a*) *Absorption from moist air*

Animals were partially desiccated by exposure to dry air at *c.* 18° C. for 1 hr.*, and allowed to recover in stirred air whose humidity was controlled at 98% by the appropriate sulphuric acid and water mixture. Woodlice of all four species continued to lose weight in these conditions.

There is little point in trying to find whether water can be absorbed from humidities higher than this. Apart from the considerable experimental difficulties, woodlice in natural conditions exposed to humidities above 98% are also likely to

* In what follows, a 'desiccated' animal means one which has suffered this treatment, not a completely dry specimen.

be exposed to liquid water, as a result of local condensation. For the present, then, it is sufficient to know that they are not capable of increasing their water content by absorbing water vapour even in relative humidities as high as 98 %.

(*b*) *Absorption of liquid water*

Desiccated woodlice were exposed for 90 min. to filter-paper liberally moistened with a dilute solution of eosin in water, in a Petri dish. They were then dissected to expose the gut, when imbibition, if it had occurred, was revealed by a red colour.

Colour was never seen in the mid-gut, but the wall of the mid-gut is more opaque than that of either the fore- or the hind-gut, so that it was impossible to be sure that no water had passed into or through this region. Consequently, the presence of red colour in the hind-gut could not be taken as evidence of imbibition through the anus. However, when the mouth was blocked, by electro-thermal cautery, no colour at all was ever seen in the fore-gut, so that a red hind-gut in these circumstances was conclusive evidence of anal imbibition. On the same grounds, the presence of red colour in the fore-gut was evidence of oral imbibition. The obvious step of blocking the anus was attempted, but it is a more difficult operation, calling for extensive cautery in order to ensure success, and only a small proportion of animals survived. Anal blockage was therefore discarded as unsatisfactory. The results of these experiments are shown in Table 1.

Table 1. *The site and amount of water uptake by woodlice exposed to free eosin water for 90 min. after desiccation in dry air at approximately* 18° C. *for* 1 *hr.*

Species	Condition	No. of animals used	Colour (denoting absorption of water) present in				Gain in weight as % of post-desiccation weight. Mean of 12 records and standard deviation	Remarks
			Fore-gut only	Hind-gut only	Both	Neither		
Ligia oceanica	Intact	17	Nil	12	4	1	3·8 (1·9)	All gained
	Mouth blocked	27	Nil	19	Nil	8	2·3 (1·7)	1 lost, 1 showed no change
Oniscus asellus	Intact	41	21	Nil	18	2	6·4 (3·0)	All gained
	Mouth blocked	40	Nil	32	Nil	8	1·8 (2·3)	3 showed no change
Porcellio scaber	Intact	35	14	Nil	20	1	2·2 (1·0)	All gained
	Mouth blocked	32	Nil	26	Nil	6	4·6 (4·1)	All gained
Armadillidium vulgare	Intact	10	3	Nil	7	Nil	4·3 (2·2)	All gained
	Mouth blocked	7	Nil	6	Nil	1	3·9 (1·6)	All gained

In order to estimate the amount of water absorbed, twelve animals of each species, and with either free or blocked mouthparts, were marked individually and weighed after desiccation and again after 90 min. exposure to eosin water. Before the second weighing they were carefully dried to remove externally adherent water. Drying, which was done with filter-paper, introduced an error in successive test weighings of less than 0·5 % of the original weight in either direction, and it may therefore be neglected.

The results of these experiments are also shown in Table 1. All the animals which were weighed before and after exposure to free water showed an increase in weight, whether the mouth was blocked or not. As regards the site of absorption, animals of each species were capable of imbibing water through the mouth and through the anus, since at least some intact animals showed a red fore- and hind-gut, whereas animals with the mouth blocked never showed colour in the fore-gut though the hind-gut was frequently coloured. Absorption through the anus was much more common than through the mouth in *Ligia*, while the reverse was true of the other three species, for no intact specimen of *Ligia* showed a red fore-gut only, and no intact specimen of the other species showed a red hind-gut only.

A parallel series of experiments was carried out on recently killed animals, but they showed no signs of imbibition into any part of the gut—the process was therefore an active one, not a passive capillary flow.

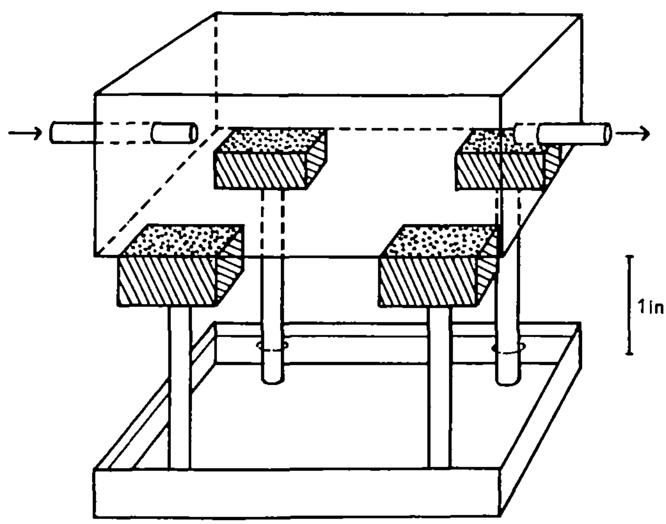

Fig. 1. Perspex container, through which a stream of air may be passed. Four plaster surfaces are let in to the floor and kept damp by capillary suction of water from below.

(*c*) *Absorption from damp surfaces*

Desiccated animals, some with free and some with blocked mouthparts, were weighed and exposed for 90 min. to damp plaster surfaces let in to the floor of a Perspex box through which a slow stream of unsaturated air (*c*. 85 % R.H.) was passed. Four plaster surfaces were provided, each approximately 1 in.^{2} in area; the capillary spaces in the plaster were permanently filled from a source of water underneath. The apparatus is shown in Fig. 1. So far as hygrometric factors are concerned, it probably imitates natural conditions reasonably well.

The results are contained in Table 2, and it is clear that intact animals of all the species used, save *Ligia*, gained weight by absorption of water. They were in good condition after such exposure, even when it was prolonged for several hours.

Animals with blocked mouths all lost weight, but it cannot be said on these grounds alone that no water was imbibed through the anus, for such absorption might be small and masked by transpiration. However, no evidence of anal imbibition was found when coloured water was used in this experiment, neither was there any increase in weight if blocked animals were exposed to plaster in saturated air. It can, therefore, be stated with confidence that imbibition in these conditions occurred by mouth only.

Table 2. *Change in weight of woodlice exposed to damp plaster surfaces in slowly moving air at approximately* 18° C. *and* 85 % R.H.

Species	Condition	No. of animals showing			Mean (and standard deviation) change in weight as % of post-desiccation weight
		Loss	No change	Gain	
Ligia oceanica	Intact	9	Nil	1	−1·5 (0·3)
	Mouth blocked	10	Nil	Nil	−6·5 (2·4)
Oniscus asellus	Intact	Nil	Nil	15	+4·5 (2·4)
	Mouth blocked	10	Nil	Nil	−6·3 (4·0)
Porcellio scaber	Intact	Nil	Nil	10	+3·3 (1·6)
	Mouth blocked	12	Nil	Nil	−2·7 (1·0)
Armadillidium vulgare	Intact	Nil	Nil	13	+4·0 (2·0)
	Mouth blocked	8	4	Nil	−1·4* (0·5)

* Those which showed no change are included in this mean.

In *Ligia* there was a loss of weight even in intact animals. This may result partly from the fact that *Ligia* normally absorbs water through the anus, and (as in the other three species) is unable to do so unless a free surface of liquid water is available. But this is unlikely to be the complete answer, for one specimen actually gained weight. It is likely that the loss of water by transpiration from *Ligia* in these conditions is usually greater than the gain of water from a damp surface, whereas in the other species the reverse is true. It is known (Edney, 1951) that *Ligia* loses water by transpiration more rapidly than the other species, and it is suggestive that the other three species stand in the same order as regards loss of weight in the present experiments as they do in respect of the transpiration rates established earlier.

Control experiments were again performed, using dead animals, and these all showed a loss of weight even though left in contact with the damp surface. Imbibition from damp surfaces is, therefore, an active process, as is the absorption of free water.

Intact animals which were exposed in the same box, but with dry plaster surfaces, continued to lose weight and eventually died. It can therefore be said that the presence of a damp surface is sufficient to ensure survival, even though the surrounding air is unsaturated.

(*d*) *Absorption through the integument*

An attempt was made to find whether water can be absorbed through the integument. The method adopted was to cauterize both mouth and anus and then to expose the animals to eosin water. As mentioned above, the effective blocking of the anus necessitates rather extensive cautery, and the small number of animals which survived the double operation were not always in good condition. They were weighed and exposed to eosin water, however, with the following results: Of fifteen *Porcellio scaber*, fourteen showed a mean gain of 2·5 % and one a loss of 1·5 %; of ten *Oniscus asellus*, three showed a mean gain of 2·2 %, five showed no change, and two showed a mean loss of 2 %; of six *Ligia oceanica* three showed a mean gain of 2·3 % and three a mean loss of 1·7 %. There is, therefore, little evidence either way, and the experiment was discontinued until a more satisfactory technique could be devised.

DISCUSSION

There are several statements in the literature to the effect that different species of woodlice inhabit environments of different degrees of dryness (refs. in Edney, 1954). Heeley (1941 *b*, 1942) went so far as to state that the distribution of different species could be predicted from a knowledge of the humidity of the surroundings. The same author (1941 *a*) stated that in the laboratory the optimum humidity for survival of various species varied from 84 % (*Trichoniscus pusillus*) to 65 % (*Armadillidium vulgare*).

It has been difficult to reconcile these observations with the results of Miller (1938) and Edney (1951). The former measured the period of survival of several species in different saturation deficits and found that 100 % R.H. was optimum at all temperatures for all species. This is not true for really high temperatures near the lethal point, for it has been found (Edney, 1951) that survival is increased, at any rate for short periods, in unsaturated air, because evaporation then lowers the body temperature. It remains true, however, that all species lose water by transpiration in all but saturated air. Miller suggested that woodlice retire by day to cool damp crevices where the air is saturated, and emerge only at night when the air temperature falls and the saturation deficit is therefore low. No doubt this is an important part of the answer.

The results of the present experiments take us a step further, for they show that although water is lost in unsaturated air, the balance may be restored by imbibition, through the mouth at least, from damp surfaces. Evidence is insufficient at present to say how damp the surface must be, or what air humidity is thus rendered tolerable. It seems likely however (and there is some supporting evidence in the present work) that given a damp surface, species which lose less water by transpiration, such as *A. vulgare*, will be able to balance imbibition against transpiration in greater saturation deficits than others. This may go some way towards explaining the various optimum humidities found by Heeley for different species, for his woodlice were living in Petri dishes and were provided with moist food from time to time. The humidity was only controlled approximately, however, by adding drops of water to the substrate of filter-paper, so that his figures must be accepted with caution.

In conclusion, it is in our view misleading to speak of certain species of woodlice as living in dry surroundings. Until precise measurements of temperature and humidity in the micro-habitats of woodlice have been made, there can be no full understanding of the ecological situation; but instead of 'dry-living' and 'wet-living' species, it is probably nearer the truth to say that all species of woodlice are confined for the most part to micro-habitats where the saturation deficit is low and damp surfaces are available, but that they differ from each other in tolerance of suboptimal conditions, both as regards degree of adversity and period of exposure.

SUMMARY

1. Experiments were undertaken to determine the site of water uptake, and the conditions in which it occurs, in *Ligia oceanica*, *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*.

2. Besides absorbing water with moist food, all four species were capable of active imbibition of water through both mouth and anus when a free water surface was available. In *Ligia oceanica*, imbibition occurred largely through the anus, in other species, through the mouth. Absorption through the anus was demonstrated by blocking the mouth by electro-cautery.

3. All species save *L. oceanica* could imbibe water through the mouth from a damp surface (plaster of Paris) sufficiently rapidly to counteract the effect of transpiration from the integument in air at *c.* 85 % R.H. No water was absorbed through the anus in these conditions.

4. The results help to resolve certain conflicting statements regarding the distribution of different species in the field. All species are for the most part 'wet living', but they differ as regards tolerance of suboptimal conditions.

This work was carried out while J. E. Spencer was in receipt of a grant from the Department of Scientific and Industrial Research.

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