

WATER RELATIONS OF SOME WOODLICE (ONISCIDEA) FROM ARID AND MESIC ENVIRONMENTS

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ABSTRACT

The desert woodlouse *Porcellio evansi* from Bahrain and Qatar has a transpiration rate as low or lower than recorded from other desert species. The synanthropic mesic *Porsellionides pruinosus* has a much higher rate, while the temperate region pill woodlouse *Armadillidium vulgare* has a rate that is intermediated between those of the other two species. It is lower in recently killed than in living specimens, and lower still in dead, rolled-up individuals.

INTRODUCTION

The water relations of woodlice (Isopoda: Oniscidea) have been studied extensively during the past 35 years or so, and the subject has been reviewed on a number of occasions (Edney, 1954, 1960, 1968; Sutton, 1972; Cloudsley-Thompson, 1977). It is of particular interest because, although the Isopoda are predominantly aquatic, the order includes those crustaceans not successfully to have made the transition from the sea land. Woodlice have a world-wide distribution. This includes the arid regions of North America (Warburg, 1965a) and Southern Australia (Warburg, 1965b), and the Great Palaeartic Desert (Cloudsley-Thompson, 1956).

The most important physiological problem facing terrestrial arthropods is undoubtedly the prevention of dehydration, the dangers of which are especially great for small animals with correspondingly large surface-to-volume ratios.

Although woodlice appear to avoid desiccation by means of behavioural responses that restrict them to moist environments (Cloudsley-Thompson, 1977; Edney, 1977), they nevertheless exhibit a range of rates of water loss by transpiration which can be correlated with various habitats. For example, the littoral *Ligia oceanica* (L.) loses water nearly seven times more rapidly than does the desert woodlouse *Venezillo arizonicus* Mulaik & Mulaik (Edney, 1977), while terrestrial isopods provide an interesting series exhibiting increasing morphological and physiological adaptations to terrestrial life.

Again, Quinlan and Hadley (1983) studied the cosmopolitan species *Porcellio laevis* Latreille and *Porcellionides* (= *Metoponorhus*) *pruinus* Brandt in Arizona, and found that the rate of water loss from *P. laevis* was significantly higher than that from *P. pruinus* which occurs in drier localities. *P. pruinus* has also been recorded from Khartoum, Sudan (Cloudsley-Thompson, 1969), but its probable origin lies in the Mediterranean region (Vandel, 1962) whence it has been distributed widely by human activities.

Studies on the water relationships of arthropods have usually employed saturation deficiency as a parameter whereby the effects on transpiration of both this concept has, however, produced controversial interpretations; and the relative significance of saturation deficiency and the physics of transpiration has yet to be determined (Edney, 1982).

Hadley and Quinlan (1984) have nevertheless recently demonstrated a relatively linear increase in water loss with increasing temperature from both living and dead *Porcellio laevis*, which is not affected by removal of surface lipids with hexane. Physiological problems invoked in the interpretation of experimental observations such as this will not, however, be considered here.

Among insects and arachnids, death results in a marked increase in rates of water loss (Edney, 1977). In the case of woodlice, Edney (1955) stated that death had no effect upon the rate of water loss, while Bursell (1955) and Quinlan and Hadley (1983) reported decreases in rates of water loss following death.

The object of the present study has been to compare the rates of transpiration from two woodlouse species that occur in Qatar – one in man-made oases, the other in the desert – with one another and with yet a third species whose distribution does not extend to desert regions, but which is well adapted to drier habitats in Europe and North America. We have been concerned primarily with eco-physiological and behavioural aspects of adaptation in relation to transpiration.

MATERIALS AND METHODS

Specimens of *Porcellio evansi* Omer-Cooper were collected by one of us (J.L.C.T.) from the desert in Bahrain in February, 1986, and in Qatar in April, 1986. The species is already known from Saudi Arabia and Iraq (Ferrara and Taiti, 1985). Woodlice from the oases of Qatar, collected in March and April, 1986, by J.L.C.T., were identified as *Porcellionides pruinosus* (Brandt). The third species, the pill woodlouse *Armadilliadium vulgare* (Latreille), was collected from the garden of C.C. in South London in April and May, 1986. Both this and *P. pruinosus* are synanthropic and have been introduced by man into many parts of the world (Ferrara and Taiti, 1979).

The animals were maintained at room temperature ($20^{\circ}\text{C} \pm 2^{\circ}\text{C}$ (range)) in plastic boxes containing layers of soil from the original site of collection. Leaf litter was added, and the cultures were kept moist with tap water.

The rates of water loss from the three species were determined gravimetrically. Groups of 5–10 individuals were removed from the cultures and placed in perforated metal cages in a container over moist filter paper for 24 hours before each experiment, in order to eliminate the possibility of the animals defaecating during the course of subsequent experimentation.

Woodlice were weighed with a Mettler balance, placed individually in small perforated metal cages and suspended in containers over anhydrous calcium sulphate (Dririte) in incubators at 15, 25, 30, 40 and 45°C . Specimens of *P. pruinosus* were exposed at the appropriate temperatures for 3 h before being re-weighed. At 15, 25, and 30°C , specimens of *P. evansi* were exposed for 6 h before re-weighing. At 35°C , they were re-weighed after exposure for 4 and 6 h (longer exposures were found to be necessary with this species because its rate of transpiration is so low).

Rates of water loss from *A. vulgare* during exposures of 3 h (except at 20°C when living animals were exposed for 6 h) were determined from both living and recently dead animals. The latter were killed by quick freezing at -40°C . In order to determine the effects of temperature on the rate of water loss, the animals were exposed to the various temperatures for 3 h before re-weighing.

Rates of water loss were expressed in terms of milligrams water lost per square centimeter of surface area per hour. The surface area of each individual

was calculated from its weight according to Wigglesworth's (1945) formula $S = KW^{2/3}$ where S = surface area in cm^2 , W = weight in mg, and K is a group specific constant. A value of $k = 12.4$ (previously used by Edney (1951) for *Porcellio scaber* (Latreille) was adopted.

RESULTS

Effects of temperature on transpiration

The rates of water loss by transpiration from the three species investigated are shown in Fig. 1. *P. pruinosus* showed the highest rate and *P. evansi* the lowest. The rates of transpiration from *A. vulgare* between 15°C and 30°C were closer to those of *P. pruinosus* than to those of *P. evansi*, but were nevertheless, significantly lower. The rates of evaporative water loss from *P. pruinosus* and *A. vulgare* increased linearly between 15°C and 30°C, as they did from *P. evansi* but, in the latter species, there was a marked increase above 30°C. This phenomenon did not appear in *A. vulgare*, nor was it observed in *P. evansi* when the means of water loss during the last 2h of the 6-hour experiments were plotted. The significance of this is discussed below.

Rates of transpiration measured from *P. pruinosus* and *A. vulgare* are closely comparable with those obtained by other authors in similar studies (Table 1). The rate of water loss from *P. evansi*, recorded here for the first time, was lower than that from *Heilepistus reaumuri* Audoiuin and Savigny (Cloudsley-Thompson, 1956) and from *Venezillo arizonicus* (Warbirg, 1965a), both of which are well adapted for life in arid environments.

Rates of water loss from living and dead *Armadillidium vulgare*

The transpiration rates of living and dead *A. vulgare* during 3h exposure to dry air at different temperatures are shown in Fig. (1). The anomalous low figure recorded from living specimens at 20°C can be ascribed to the fact that measurements were carried out over 6h at this temperature, but over 3h at all the other temperatures (see below). At all temperatures, the rates of water loss were greater from living than from freshly-killed animals.

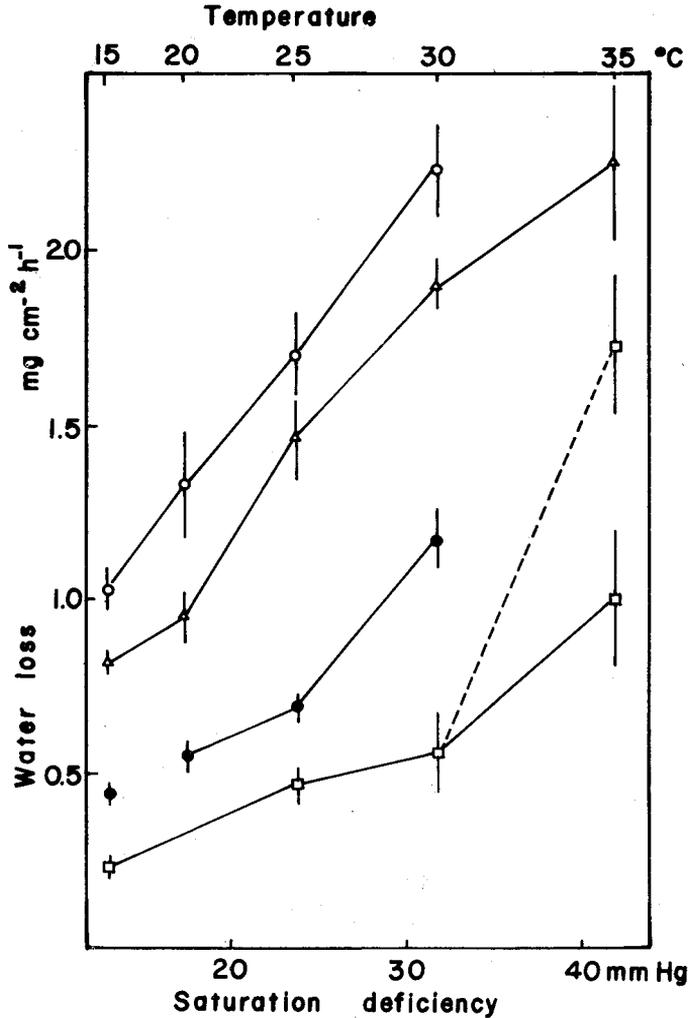


Fig. 1 : Rates of water loss at different temperatures and saturated deficiency from different species of woodlice:

- ... *Porcellionides pruinosus* (living). ● ... *A. vulgare* (freshly killed).
 △ ... *Armadillidium vulgare* (living). □ ... *Porcellio evansi* (living).

A (broken line) rate of water loss during the first 4 h exposure; B rate during the last 2 h exposure. Vertical bars indicate the Standard Errors of the means. Ordinate: Water loss ($\text{mg cm}^{-2} \text{h}^{-1}$). Abcissa: Temperature ($^{\circ}$) above, and Saturation Deficiency (mm Hg) below.

Table 1
Comparative rates of transpiration from different species of woodlice.

Species	Temperature °C	Exposure Time	Water loss ($\mu\text{g cm}^{-2} \text{h}^{-1}$ mm Hg ⁻¹)	Authority
<i>Porcellio scaber</i> (Living)	30	15 min	110	Edney (1951)
<i>Porcellionides</i> <i>pruinosis</i> (Dead)	30	1 h	68.4	Quinlan and Hadley (1968)
(Living)	24	1 h	74.6	Cloudsley- Thompson (1969)
(Living)	30	3 h	70.1	(This paper)
<i>Armadillidium</i> <i>vulgare</i> (Living)	30	30 min	70	Warburg (1965a)
(Dead)	30	3 h	36.8	(This paper)
(Living)	30	3 h	60.1	(This paper)
<i>Hemilepistus</i> <i>reaumuri</i> (Living)	19	15 min	23.7	Cloudsley- Thompson (1956)
<i>Venecellio</i> <i>arizonicus</i> (Living)	25	1 h	32	Warburg (1956a)
<i>Porcellio evansi</i> (Living)	25	6 h	19.9	(This paper)

The pattern of water loss from *A. vulgare*

- (a) Living Animals: In order to determine the progress of transpiration over time, specimens of *A. vulgare* were desiccated over periods of 5h at 25°C and their weights recorded at hourly intervals. The results, shown in Fig. 2, disclose a sharp decrease in water loss during the first two hours of exposure.

Thereafter, the rate remained almost constant. About one third of the total loss of weight took place during the first hour of exposure. In subsequent hours, evaporation fell to a level between 14.4% and 15.9% per hour (in contrast, the mean during the first two hour and 3.2% during the next two).

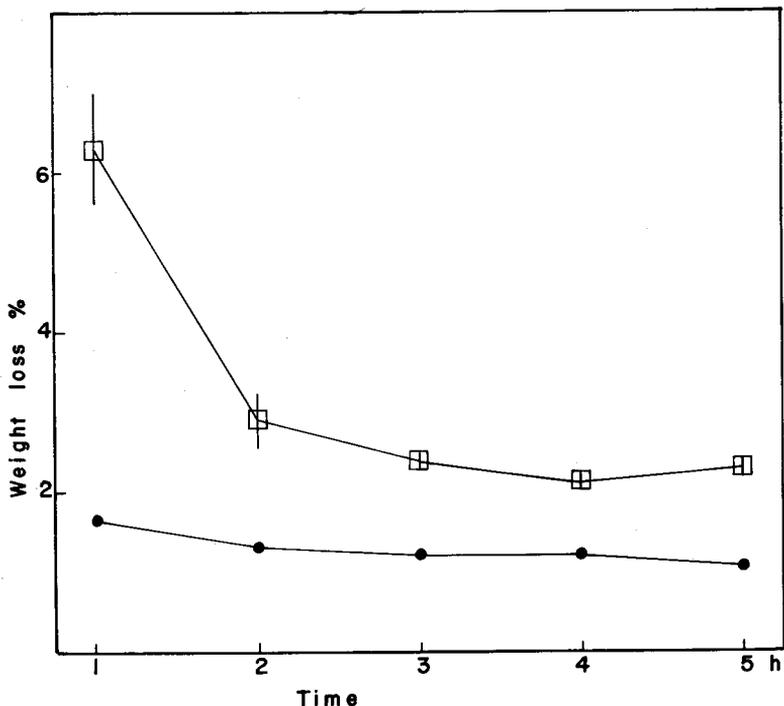


Fig. 2 : Water loss from *A. vulgare* exposed to dry air 25°C for 5h. □ ... living; ● freshly killed and glued dorsal side uppermost to a glass coverslip. Vertical bars indicate the standard errors of the means.

- (b) Dead Animals: The rates of water loss by transpiration from dead animals were significantly lower than those from living animals at all temperatures tested. Animals that had been killed and glued dorsal side up on a glass coverslip (Fig. 2), or killed and glued in a rolled-up or conglobate position (Fig.3) showed the lowest rate of water loss. Pill woodlice killed but not rolled up showed a marked decrease in their rates of water loss after the first hour's exposure (Fig.3). A similar, but a sharper drop was observed in living animals (Fig.3). On the other hand, at 25 and 35°C, water loss from

the dead, conglobate animals remained almost constant throughout hour's exposure (Fig. 3). This suggest that most of the water during the first hour of exposure may have evaporated from the respiratory surfaces of living woodlice is replaced from the maxillary glands (Hoese, 1981) may account for the difference in the amount of water lost from dead and living animals during this time. The high rate of water lost in the fourth hour, may be explained by postulating that after three hours the animals were becoming severely desiccated.

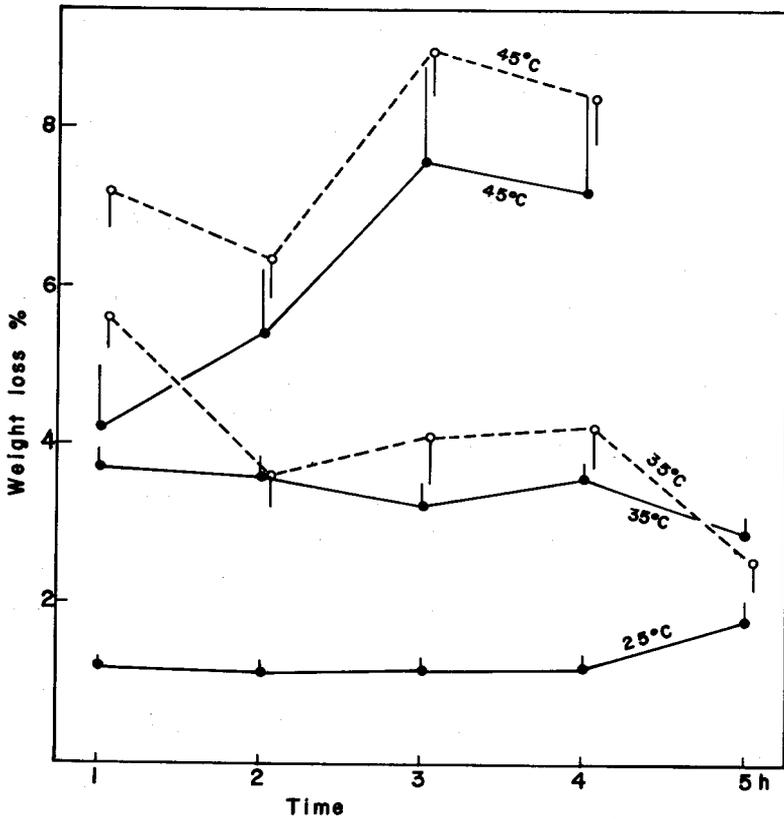


Fig. 3 : Water loss from *A. vulgare* exposed to dry air at different temperatures for 5h. ○ ... freshly killed controls. ● ... freshly killed and rolled up. Vertical bars indicating the standard errors of the means have, for clarity, been inserted on one side of each point only.

DISCUSSION

A controversy still exists regarding saturation deficiency and the physics of transpiration. The early belief that saturation deficiency controls water loss directly has shown to be simplistic (Edney, 1982). Indeed, Toolson (1978, 1980) has proposed that gradients in chemical potential, rather than gradients in water vapour activity, which corresponds with saturation deficiency, should form the basis of interpretations of experimental observations: but this hypothesis has, in turn, been criticised by Monteith and Campbell (1980) and by Gilby (1980). In any case, no "critical temperature" in the classical sense, has been demonstrated in any of the three species investigated.

The three species of woodlice under consideration do, however, show differing degrees of adoption to dry conditions: water loss through transpiration is greatest in the mesic *P. pruinus* and lowest in the xerophytic *P. evansi*. It is lower in recently killed *A. vulgare* than in living animals, and lower still in dead, rolled-up specimens.

A considerable increase in the rate of transpiration from *P. evansi* was recorded at temperature above 30°C (Fig. 1), but most of this occurred during the first 4h of exposure and even so was considerably less than that from *P. pruinus* or *A. vulgare*. This increase is not sufficient, in our opinion, to justify invoking the concept of a "critical temperature".

A complication in assessing the significance of water loss by evaporation from woodlice is due to the fact that the respiratory pleapods are always kept moist. Urine from the glands is conducted to them by a series of capillary channels (Hoese, 1981) and is reabsorbed by being taken in through the rectum. In addition to facilitating respiration, this permits the excretion of nitrogen in the form of ammonia gas. The circulation of water on the ventral surface of woodlice between the excretory organs and the anus means that assessments of permeability through the cuticle are probably all too high, since conversion from measured rates of transpiration to calculated permeability do not take into account water which has not passed through the integument. At the same time, it does explain the reduction in figures for evaporation obtained from *A. vulgare* in the conglobate state. In nature, of course, flattened woodlice, such as *Porcellio* and *Porcellionides* spp. are able to reduce respiratory transpiration by pressing their ventral surfaces against the substrate.

The success of the Palaearctic desert woodlouse *Hemilepistus reaumuri* depends to a considerable extent upon its social behaviour and burrowing habits (Shachak, 1980; Coenen–Stass, 1984; Linsenmair, 1984). Water loss through transpiration is compensated for, both by cutaneous absorption of moisture and by the ingestion of damp sand. When cutaneous absorption increases, ingestion of damp sand is reduced. The existence of the water-saturated air in the burrow is a limiting factor in the distribution of both *H. reaumuri* and *H. aphganicus* Borutzky in arid areas (Coenen–Stass, 1981). Desiccation induces a distinct increase in blood osmolarity and the concentration of ions, especially Na + (Coenen–Stass, 1981). Other species of terrestrial isopods do not exhibit such high osmotic values. Despite tolerance of a wide range of osmotic concentrations, there is evidence of active osmotic regulation by *H. reaumuri*, especially of Na + concentration (Coenen–Stass, 1985). At the same time, water vapour can be absorbed from the air (Coenen–Stass, 1981). Comparable information regarding *P. evansi*, *P. pruinosus* and *A. vulgare* is not available, but it seems probable that the physiology of the water relationships of these species will prove to be equally complex. Certainly, Price and Holdich (1980) found that *Armadillidium depressum* shows better control of osmotic pressure during progressive desiccation than does *Porcellio scaber*; whereas *Oniscus asellus*, which shows absolutely no ability for osmoregulation, water is lost exclusively from the blood without any supplementation from the tissues (Holdich and Mayes, 1976).

SUMMARY

Rates of transpiration from three species of woodlice have been compared. They were highest in the synanthropic *P. pruinosus* from man made oases in Qatar and lowest in *P. evansi* from desert regions of Qatar and Bahrain. They were as low or lower in this species than the rates previously recorded from the better known desert woodlice *Hemilepistus reaumuri* and *Venezillo arizonicus*. Water loss from the temperature region pill woodlouse *A. vulgare* was intermediate, and significantly different from that of the other two species. It was lower in recently killed specimens than in living animals and lower still in dead rolled-up specimens and dead animals glued ventral side down to glass coverslips.

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العلاقات المائية لبعض أنواع من قمل الخشب (أوتيسيديا) من بيئات قاحلة وبيئات أخرى

س. كونستانتينو و ج. ال. كلودزلي تومسون

وجد أن معدل بخر الماء لقمل الخشب الصحراوي من نوع (بورسليو ايفانسي) الموجود في كل من دولة البحرين ودولة قطر مماثل في قوته أو أقل من المعدل المعروف لبعض الأنواع الصحراوية الأخرى . كما لوحظ أن في النوع (بورسيلونيوس بروينيوس) من المناطق الأقل جفافاً أن معدل البخر أعلى بكثير بينما كان هذا المعدل في قمل الخشب القرص (أرماديليديم فيلجاري) من المناطق المعتدلة متوسطاً بين النوعين الآخرين .

ولوحظ كذلك أن معدل البخر بصورة عامة في العينات التي قتلت حديثاً أقل منه في العينات الحية وأقل من ذلك في الأفراد الميتة المغلفة .