Body Shape in Terrestrial Isopods: A Morphological Mechanism to Resist Desiccation?

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ABSTRACT   Woodlice are fully terrestrial crustaceans and are known to be sensitive to water loss. Their half-ellipsoidal shapes represent simple models in which to investigate theoretical assumptions about organism morphology and rates of exchange with the environment. We examine the influence of surface area and mass on the desiccation rates in three eco-morphologically different species of woodlice: *Oniscus asellus*, *Porcellio scaber*, and *Armadillidium vulgare*. Our analysis indicates that the rate of water loss of an individual depends on both the initial weight and the body surface area. Interspecific and intraspecific analyses show that the mass-specific water loss rate of a species decreases along with the ratio of surface area to volume. In particular, we show that body shape explains the difference in mass-specific water loss rates between *A. vulgare* and *P. scaber*. This observation also explains several known ecological patterns, for example, the distribution and survivorship of individuals. However, in addition to body size and shape, water loss in terrestrial isopods depends also on the coefficient of permeability (i.e., a measure of water loss rate per surface unit), which is high in *O. asellus* and lower (and at similar levels) in *P. scaber* and *A. vulgare*. We discuss morphological, physiological, and behavioral aspects of water loss avoidance in terrestrial isopods. J. Morphol. 276:1283–1289, 2015.
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INTRODUCTION

All organisms continually exchange various resources (e.g., nutrients, oxygen, and water) and energy with their environment, either by passive or active processes. Supported by a strong theoretical and empirical framework (Schmidt-Nielsen, 1984; Calder, 1996; Banavar et al., 2014), it is accepted that the lower the surface area-volume ratio of an organism, the lower its capacity to passively exchange energy or matter with its surroundings, and conversely, the higher its potential for conservation of resources. Therefore, natural selection leads to variations in the potential amounts of resources conserved and energy exchanged by organisms, that is, in body shape and size, according to environmental characteristics (Meiri and Dayan, 2003; Chown and Gaston, 2010; Gardner et al., 2011).

For any terrestrial organism, control of water loss is a subject of particular importance because desiccation stress is a major constraint on its physiological functions. In particular, many intertidal or fully terrestrial invertebrates such as mollusks or arthropods are confronted with more or less chronically dry conditions. Water loss in invertebrates may be caused by cuticular transpiration, respiration, or excretion (Chown and Nicolson, 2004). Adaptive mechanisms related to desiccation resistance have been described, including the limitation of water loss, the increase in desiccation tolerance, and the increase in water storing capacity (e.g., Chown and Nicolson, 2004; Benoit, 2010; Chown et al., 2011). For example, production of cuticular and integumental lipids (quantity, composition) can form an effective waterproofing barrier to maintain water balance in many arthropods (e.g., Gibbs, 1998; Benoit, 2010). In other respects, difference in desiccation resistance between species may be due to body size more or less associated with body water content (Le Lagadec et al., 1998; Gray and Bradley, 2005; Fouet et al., 2012; Tejeda et al., 2014). In addition, individual behaviors such as active water vapor absorption (Wright and Machin,

1993; Chown and Nicolson, 2004) and collective behaviors such as aggregation (decreasing individual surface area and/or increasing local humidity in groups) can also reduce individual rates of water loss in many arthropods (Yoder et al., 2002; Benoit et al., 2005; Broly et al., 2014). These mechanisms of desiccation resistance, whether morphological, physiological, or behavioral, are not mutually exclusive. Understanding their diversity and how they act, alone or in synergy, is of primary importance for understanding the terrestrialization observed in arthropods.

Among arthropods, Isopoda (Crustacea) inhabit a great variety of environments, from marine to land (Warburg, 1993; Wilson, 2008; Poore and Bruce, 2012). Oniscidea, terrestrial isopods commonly known as woodlice, are represented by more than 3,600 species. Oniscidea is the largest fully terrestrial group within the crustaceans. Because of this and because they are particularly abundant in soils, during the past century, woodlice have been the focus of numerous studies and discussions about their terrestrialization (Allee, 1926; Edney, 1954, 1968; Cloudsley-Thompson, 1988; Warburg, 1993; Hornung, 2011). Notably, these studies have highlighted that oniscidean physiological adaptations to land are poor in contrast to those of insects, particularly due to their negligible amounts of cuticular lipids (Hadley and Quinlan, 1984; Compere, 1991; Vittori and Štrus, 2014) and their lack of a tracheal system (Schmidt and Wägele, 2001). Consequently, the rate of water is important in woodlice, primarily because of their passive ventral and dorsal cuticular transpiration (Edney, 1951; Dias et al., 2013). Quite obviously, water loss rate in woodlice varies according to temperature and humidity of the environment (Edney, 1951, 1968).

An interesting observation in isopods is a tendency toward antero-posterior shortening in terrestrial forms when compared with aquatic taxa, suggesting that morphological variations may be important during the terrestrialization process and especially for desiccation processes. Although the range in body water content is relatively small among terrestrial isopod species (between 60 and 70% of the fresh body weight; Warburg, 1993; Greenaway and Warburg, 1998), the water loss rate and desiccation resistance vary widely among species (Dias et al., 2013). In this study, we hypothesize that body size and body shape may be involved in this interspecific variation.

Many studies addressing the surface area and volume of organisms do not present data on these two variables because surface area and volume are difficult to measure accurately in complex organisms. Often, these characteristics are extrapolated from body mass, although the surface area-volume ratio depends not only on the absolute volume of the individual but also on the individual shape. Here, we utilize the simple form of a woodlouse (approximated by a half-ellipsoid) to i) calculate surface area and volume values and ii) relate the body shape and body size to the water loss rate in three common species of woodlice.

We compare *Oniscus asellus*, *Porcellio scaber*, and *Armadillidium vulgare*, which are three species of particular interest because of the continuum of terrestrialization adaptations they exhibit and because of their frequent use in various experiments since the early works of Edney (1951). From an allometric viewpoint, these species have the advantage of exhibiting the same body shape pattern; however, their body proportions vary according to species.

MATERIALS AND METHODS
Animals

Woodlice were collected in various localities in northern France (Lille, Bois-Grenier, and Ambleteuse). The three most common species were trapped: *O. asellus* Linnaeus, 1758; *P. scaber* Latreille, 1804; and *A. vulgare* Latreille, 1804. Within Oniscidea, the three species belong to Crinocheta Legrand, 1946- (Schmidt, 2008). In the field, *O. asellus* inhabits hygric-mesic habitats, *P. scaber* mesic habitats, and *A. vulgare* mesic-xeric habitats.

Specimens were maintained under laboratory conditions (22°C, natural photoperiod of the region) during the experimental period (approximately 1 month from May to June). Young (i.e., unsexable), molting individuals, and ovigerous females were excluded.

Water Loss

To determine the water loss rate of the woodlice, 150 individuals (75 males and 75 females) of each species (*O. asellus*, *P. scaber*, *A. vulgare*) were used. Each individual was placed in an open glass jar ($\varnothing$ 64 mm diameter) with a fine mesh screen lining the bottom so that the individual could get back on its legs if overturned. Each individual was weighed at the beginning of the experiment and then placed in its jar in the dark in a BD240 incubator (Binder GmbH, Tuttlingen, Germany) at $20.09 \pm 0.25°C$ with a relative humidity (RH) of $46.71 \pm 2.79\%$. After 1 h of experimentation, individuals were removed from the incubator and weighed again. Woodlice were weighed with an Explorer E01140 balance (Ohaus Corp., NJ; precision $d = 0.1$ mg). The rate of weight loss is considered to be the water loss that occurred during the hour of experimentation.

We ensured that *A. vulgare* did not present spontaneous conglobation behavior during the experiments (see Smigel and Gibbs, 2008).

Surface Area-Volume Ratio

To calculate the surface area-volume ratio of the woodlice and correlate that ratio to water loss, we used the same individuals previously weighed to determine the water loss rate ($n = 150$ individuals for each species; see above). The body length (excluding antennae and uropods, from the tip of the cephalon to the end of the telson), maximal width and maximal height (excluding legs) of each woodlouse were measured (Fig. 1) with an electronic sliding caliper (Kingfisher, London, UK; precision $d = 0.02$ mm). All individuals were also photographed as viewed from above. The surface area of each woodlouse on the ground (i.e., the surface area of the ventral region) was calculated by counting the number of pixels occupied by the woodlouse (using Photoshop 7.0.1, Adobe Systems Software,
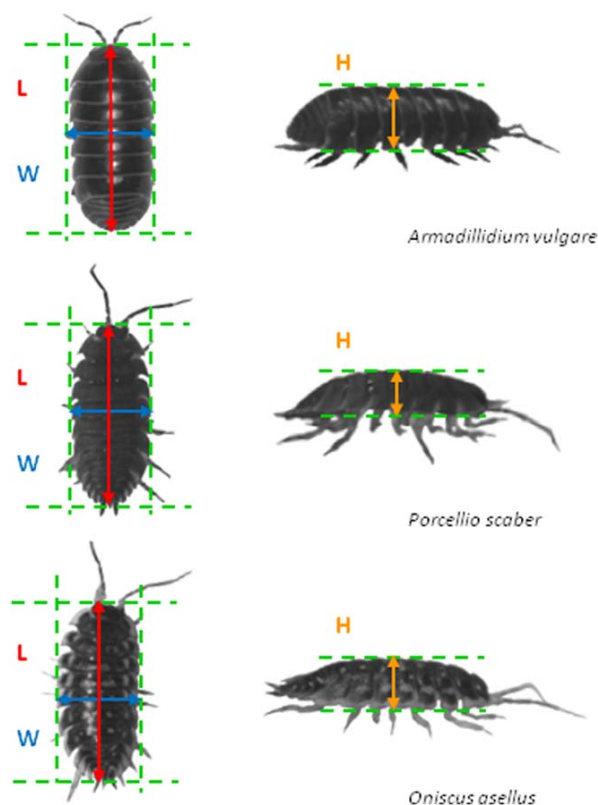
Fig. 1. Diagrammatic depiction of measurements of the maximal body length (red), width (blue), and height (yellow) in the three species.

Fig. 2. Box plot of weight loss rate per unit of body mass (*g* loss/*g* fresh weight) in the three woodlouse species *O. asellus*, *P. scaber*, and *A. vulgare* after 1 h at $20 \pm 0.2°C$ and RH $46 \pm 2.8\%$. The indicator "*" denotes statistically significant differences between species.

Ireland) and then compared with the number of pixels occupied by a reference with a known surface area (cm²).

Each woodlouse was assumed to be a half-ellipsoid (see Supporting Information Fig. S1). We excluded the legs and antennae. The total surface area of a woodlouse exposed to air (*S*) was approximated using Knud Thomsen's formula:

$$S \approx \frac{\left(4\pi \left(\frac{a^p b^p + a^p c^p + b^p c^p}{3}\right)^{\frac{1}{p}}\right)}{2} + \varnothing, \qquad (1a)$$

where *a* is half of the woodlouse length, *b* the half-width, and *c* the height. $\varnothing$ is the surface area of a woodlouse on the ground (measured; see above). $p \approx 1.6075$.

The control for the measurement of $\varnothing$ is given in Supporting Information Figure S2.

The volume of a woodlouse (*V*) is approximated by the half-volume of an ellipsoid:

$$V = \frac{\frac{4\pi abc}{3}}{2} \qquad (1b)$$

Statistics

To compare nonlinear data, we performed linear regression on log-transformed data. Figures and regressions were obtained with GraphPad Prism 5.01 (GraphPad Software, La Jolla, CA). Statistical tests were performed with Past 2.17. The ellipses were drawn with CorelDRAW® Graphics Suite - Version 12.0 software (Corel Corp., Ottawa, Canada).
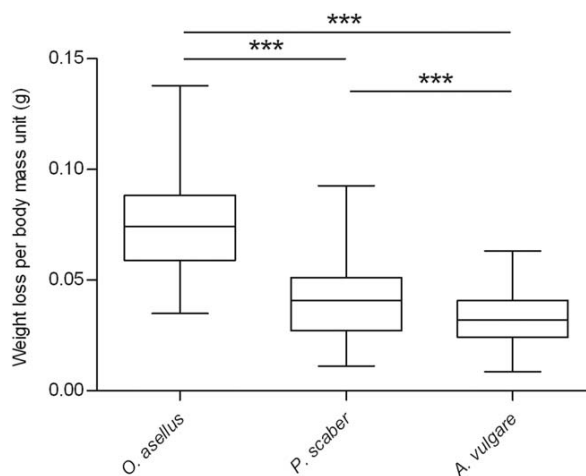
RESULTS

The weight-loss data meet the requirements of a parametric statistical test: normality (Kolmogorov–Smirnov test; $KS \leq 0.051$; $P > 0.1$ for all the species) and sample size ($n = 150$). The weight loss per unit body mass of the three species is significantly different after 1 h of the experiment (ANOVA; $F = 290.6$; $P < 0.001$; Fig. 2). A Tukey-Kramer multiple comparison test indicates that the rate of weight loss in *O. asellus* is significantly higher than in *P. scaber* (Fig. 2; $q = 25.224$; $P < 0.001$) and *A. vulgare* (Fig. 2; $q = 31.069$; $P < 0.001$). Additionally, weight loss in *P. scaber* is significantly higher than in *A. vulgare* (Fig. 2; $q = 5.846$; $P < 0.001$).

Second, we calculated the surface area and volume of woodlice using measurements of the length, width and height of the animals, assuming that a woodlouse is a half-ellipsoid.

The relationship between the surface area (*S*) and the volume (*V*) of individuals in the three species (Fig. 3a) follows the power law.

There are linear relationships between the length, the width, and the height of individuals in the three species (see Supporting Information Fig. S3). Combining these linear relationships and the equations for *S* (Eq. 1a) and *V* (Eq. 1b), we obtain:

$$S = AV^{2/3} \qquad (2a)$$

with

$$A = \pi \left(2\left(\frac{\beta^p + \gamma^p + (\beta\gamma)^p}{3}\right)^{1/p} + \beta\right)\left(\frac{3}{2\pi\beta\gamma}\right)^{2/3} \qquad (2b)$$

The complete proof of *S* being proportional to $V^{2/3}$ is provided in the Supporting Information.
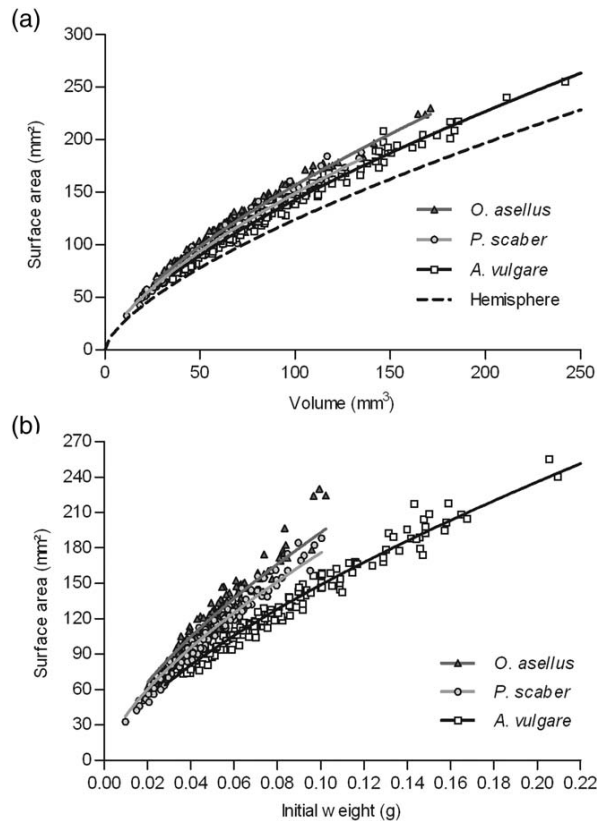
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(a)

(b)

Fig. 3. **(a)** Relationship between the surface area (mm^2) and volume (mm^3) of the body in *O. asellus*, *P. scaber*, and *A. vulgare* ($n = 150$ individuals for each species) and for a theoretical perfect hemisphere. Solid lines represent the nonlinear regression of the scatter plots for the three species (see Table 1). **(b)** Relationship between the surface area (mm^2) of the body and initial weight in *O. asellus*, *P. scaber*, and *A. vulgare* ($n = 150$ individuals for each species). Solid lines represent the nonlinear regression of the scatter plots for the three species (see Table 1).

For the three investigated isopod species, weight is proportional to volume (see Supporting Information Fig. S4). Therefore, the body surface area (S) is also proportional to the body weight (W) (Fig. 3b).
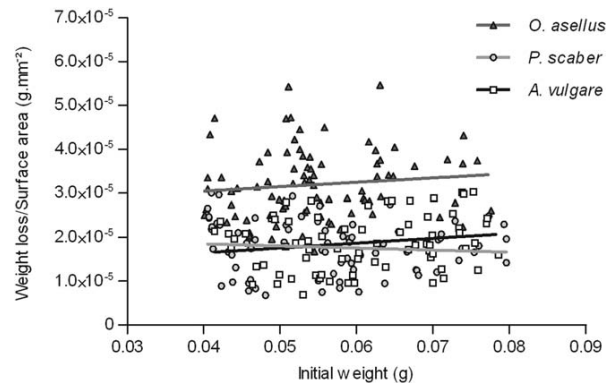

Fig. 4. Relationship between the weight loss per body surface area unit (g mm^{-2}) and the initial fresh weight of individuals of *O. asellus* ($n = 87$ individuals), *P. scaber* ($n = 75$), and *A. vulgare* ($n = 74$). For the three species, only individuals of the same weight range were included to allow relevant comparisons. Solid lines represent the linear regression of the scatter plots for the three species.

$$W = \delta V \qquad (3a)$$

$$S = \frac{A}{\delta^{2/3}} W^{2/3} = BW^{2/3} \qquad (3b)$$

Parameter values of A, δ, and B are given in Table 1.

A one-way ANCOVA on the logarithmic data presented in Figure 3a,b indicates significant differences in the adjusted means of the regressions between *O. asellus* and *P. scaber* (Fig. 3a: $F = 98.75$, $P < 0.0001$; Fig. 3b: $F = 153.3$, $P < 0.0001$), between *P. scaber* and *A. vulgare* (Fig. 3a: $F = 84.39$, $P < 0.0001$; Fig. 3b: $F = 517.3$, $P < 0.0001$), and between *O. asellus* and *A. vulgare* (Fig. 3a: $F = 408.1$, $P < 0.0001$; Fig. 3b: $F = 1,090$, $P < 0.0001$).

Figure 4 shows the relationship between weight loss per unit of body surface area (C) and initial weight for individuals of similar size. None of the slopes of regression in Figure 4 is significantly different from zero (F test; $0.6289 < F < 2,818$; $0.0976 < P < 0.4304$), and each regression is statistically similar to the others (one-way ANCOVA test;

TABLE 1. *For the three species, values of A calculated (Eq. 2) from the relationship between the surface area of the body and volume; δ fitted from the relationship between initial weight of individuals and body volume (see Supporting Information Fig. S4); values of B calculated (Eq. 3) and fitted (control) from the relationship between the surface area and body weight (see Fig. 3b); mean values of the weight loss per unit of surface (C; Eq. 4) for the three species and the product of this constant with the surface per unit of weight (calculated B × C)*

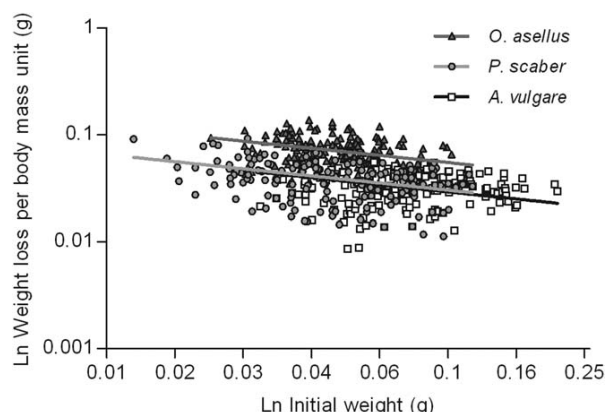|	A calculated	δ fitted (CI 95%)	B calculated	B fitted (CI 95%)	C mean (SD)	CB calculated
O. asellus	6.98	0.0007154 (0.0007022–0.0007287)	872.6	895.6 ($R^2 = 0.92$) (885.0–906.3)	0.000032 (7.9×10^{-6})	0.028
P. scaber	6.59	0.0007688 (0.0007572–0.0007805)	785.2	815.9 ($R^2 = 0.96$) (807.7–824.1)	0.000020 (8.0×10^{-6})	0.016
A. vulgare	6.40	0.0009341 (0.0009213–0.0009470)	669.7	690.0 ($R^2 = 0.97$) (684.3–695.7)	0.000021 (8.0×10^{-6})	0.014

Fig. 5. For the three species ($n = 150$), the logarithmic relationship between the weight loss per unit of body mass (g loss/g fresh weight) and initial weight. Solid lines represent the data fitting by the Eq. 5.

$F = 1.583$, $P = 0.2077$). Therefore, the weight loss is constant per unit of surface and can be expressed by the adjusted mean of regression regardless of the animal's weight. The adjusted mean for *O. asellus* is significantly higher than those of *P. scaber* ($F = 156.3$; $P < 0.0001$) and *A. vulgare* ($F = 135.1$; $P < 0.0001$). The adjusted means of regression of *P. scaber* and *A. vulgare* are not significantly different ($F = 0.4957$; $P = 0.4825$). These constants (C) are given for the three species in Table 1.

Finally, we obtain the following relationship expressing the water loss rate of a woodlouse as a function of its initial weight (W), of its surface (B) and of a specific constant of weight loss per unit of surface (i.e., mean coefficient of permeability of the body; C):

$$\Delta W = CS = CBW_i^{2/3} \tag{4}$$

The product CB of Eq. 4 increases from *A. vulgare* to *O. asellus* (Table 1). This last equation also gives the following equation for the relative water loss:

$$\frac{\Delta W}{W_i} = CBW_i^{-1/3} \tag{5}$$

The data fitted by this equation are presented in Figure 5.

For the three species, the weight loss per unit of body mass decreases with the initial weight: for *O. asellus* $\Delta W/W = 0.02561\ W^{-1/3}$ (CI 95% = 0.02435–0.02687), for *P. scaber* $\Delta W/W = 0.01410\ W^{-1/3}$ (CI 95% = 0.01334–0.01485), and for *A. vulgare* $\Delta W/W = 0.01359\ W^{-1/3}$ (CI 95% = 0.01286–0.01431).

DISCUSSION

Body size is a key feature of organisms because it strongly influences the amount of exchange with the environment, aspects of physiology such as

metabolic rate (Reiss, 1989; Gillooly et al., 2001; Glazier, 2014), and other features such as growth and fecundity (Honek, 1993; Blanckenhorn, 2000; Chown and Gaston, 2010). Isopoda is a remarkable crustacean group because of the wide variety of body sizes and body shapes exhibited by these species (Wilson, 2008; Poore and Bruce, 2012). Body size and body shape in terrestrial isopods have long been investigated in the context of environmental pressures such as the response to predation (notably due to the efficient defensive conglobated form of *A. vulgare*; Castillo and Kight, 2005), or (micro)habitat features (Schmalfuss, 1984; Hornung, 2011) but more rarely in the context of water loss (Tsai et al., 1998; Smigel and Gibbs, 2008).

In this study, we confirm an already well-established gradient: *A. vulgare* is the least subject to water loss, whereas *O. asellus* is the most; *P. scaber* is located between these two extremes (e.g., Edney, 1954; Dias et al. 2013). These results are consistent with the humidity preferendum of these species observed in both the laboratory and the field (Waloff, 1941; Warburg, 1968). *O. asellus* loses an average of 7.5% of its fresh weight in only 1 h, compared with 3.2% in *A. vulgare* (see Fig. 2). In contrast, under the same conditions used here, a cockroach loses a similar amount of water in one day (Chown et al., 2011). These particularly high desiccation rates make terrestrial isopods particularly interesting and highly useful for exploring the physio-morphological mechanisms involved in water loss in terrestrial arthropods.

We quantified the body dimensions of the three species studied and used these morphometric measurements to decipher the interplay between body weight, body shape, and water loss rate. Notably, we calculated the volume and surface area of individuals based on a half-ellipsoid, which provides a close approximation of the woodlouse body shape. Our results show that the body shapes of these three species cannot be considered similar. In particular, for the same volume or weight, *O. asellus* presents the highest surface area for exchange with the environment, whereas the body shape of *A. vulgare* presents the minimal surface area-volume ratio (i.e., it is the most round) and approaches a hemisphere. *P. scaber* is between these two extremes.

In an intraspecific analysis, the observed geometric scaling of surface area with body mass in each species supports a lack of a particular shape change during development. However, our results show that the lower the surface area-volume ratio of an individual, the smaller the mass-specific water loss. This experimental result partially confirms theoretical expectations. Thus, the larger an individual, the greater its volume—that is, the smaller its surface area-volume ratio is—and the less its water loss will be. Consequently, the smallest individuals (mainly the younger individuals),

which present the highest surface area-volume ratio, are more sensitive to water loss than adults. In addition to risks such as predation (Paris 1963, Sunderland and Sutton 1980), surface area-volume ratio, and desiccation rate may explain why the mortality rate is particularly high in juveniles compared to adults and why larger juveniles show a greater survivorship than smaller juveniles under moisture stress (Hassall et al., 2005). Notably, the effect of body size on desiccation resistance may explain why females invest more in offspring size than in brood size under conditions of high temperature (Brody and Lawlor, 1984; Hassall et al., 2005).

However, it is important to note the relatively high intraspecific variability in water loss observed here in the three species. Several hypotheses may explain this variability at the individual level. Water loss is most likely a passive cuticular phenomenon in woodlice; nevertheless, we cannot confirm that measured mass losses strictly reflect passive cutaneous transpiration (see Edney, 1951; Lindqvist, 1972; Wright and Machin, 1993; Greenaway and Warburg, 1998; Dias et al., 2013). Although they account for a small proportion of total water loss in woodlice, unpredictable events such as maxillary and anal urination can affect total weight loss at the individual level (Lindqvist, 1972). The individual stress level or sex may also affect metabolism and, therefore, affect metabolic water loss rate (e.g., through respiration). At last, the individuals may manage their water balance through active water vapor absorption (Wright and Machin, 1990, 1993).

In an interspecific analysis, *A. vulgare* presents the lowest average water loss rate, but its population shows an important overlap with that of *P. scaber*. In these two species, the mean body permeability (C) can be considered similar, but *A. vulgare* presents the least surface per unit of weight (B) and is also larger (in our sample and likely in natural populations). Therefore, body shape and especially body size may explain the difference in the average transpiration regime of these two species and can explain, to a high degree, why *A. vulgare* is on average the most resistant to desiccation. Although the difference between these two species appears minimal under our experimental conditions (20°C, 45% RH, 1 h of experimentation), the more efficient shape and heavier weight of *A. vulgare* could significantly increase its resistance to desiccation when exposed to high temperatures or dry environments (see Edney, 1951, 1968).

However, *O. asellus* clearly does not follow the same pattern. Certainly, its mass-specific surface area is greater than those of *P. scaber* and *A. vulgare*, explaining part of its total water loss, but its mean body permeability (C) is also greater. For individuals of similar size, *O. asellus* loses twice as much water as *P. scaber* or *A. vulgare*. There-

fore, other factors beyond body size and shape should be considered to explain the variability in the water loss rate between terrestrial isopod lineages. Several physiological factors may affect the body permeability. The complexity of respiratory organs may be involved: in particular, the simplicity of respiratory fields in *O. asellus* may explain its high water loss rate, compared to the elaborate pleopodal lungs in *P. scaber* and *A. vulgare* (Schmidt and Wägele, 2001). Additionally, the thickness of the isopod cuticle, which is a determinant of body permeability (see Fick's law), may also vary between body regions and species (Csonka et al., 2013; Vittori and Štrus, 2014) and may explain the differences observed between the three species.

To conclude, in the three species considered in this study, allometry and water loss rate are in accordance. The lower the individual surface area-volume ratio, the lower the individual water loss rate, both at the intraspecific and interspecific levels. In particular, body shape, rather than permeability, appears to explain the difference in mass-specific water loss rates between *A. vulgare* and *P. scaber*. However, some precautions must be taken with the generalization of this geometric rule. In particular, our analysis indicates that the water loss rate of an animal depends on its initial weight, on its surface area, and also on a species-specific coefficient of permeability. As with many model invertebrates and vertebrates, water loss control in woodlice is unquestionably multifactorial, consisting of morphological, physiological, and behavioral factors. For example, the occurrence and prevalence of individuals engaging in collective behaviors such as aggregation may offset physio-morphological adaptations to desiccation by decreasing the amount of surface area exposed to the environment in each individual (Hassall et al., 2010; Broly et al., 2014).

ACKNOWLEDGMENTS

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