Effects of group size on aggregation against desiccation in woodlice (Isopoda: Oniscidea)

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Abstract. Aggregation in terrestrial isopods, a behaviour that results in the formation of dense clusters, is readily accepted as a mechanism of resistance to desiccation. Thus, aggregation is considered to be an adaptation to terrestrial life in this fully terrestrial suborder of crustaceans. In the present study of *Porcellio scaber* Latreille, a cosmopolitan species, individual water loss is investigated experimentally as a function of the size of the aggregates and, for the first time, over a large range of group sizes (groups of 1, 10, 20, 40, 60, 80 and 100 individuals). From the perspective of an isolated individual, aggregation behaviour is effective in reducing the rate of water loss whatever the group size, and reduces the individual water loss rate by more than half in large groups. However, the water loss rate of an individual follows a power law according to group size. Accordingly, if the addition of individuals to small groups strongly reduces the water losses per individual, adding individuals to large groups only slightly reduces the individual water losses. Thus, the successful reduction of the water loss rate by this aggregation behaviour is confirmed, although only up to a certain limit, particularly if the number of individuals per aggregate exceeds 50–60 under the experimental conditions used in the present study. Moreover, the individual surface area exposed to the air, as a function of group size, follows a similar pattern (i.e. a similar power law). Thus, a geometrical explanation is proposed for the nonlinear water losses in woodlice aggregates. These results are discussed in relation to the group sizes observed both in the laboratory and the field.

Key words. Cluster, group size, *Porcellio scaber*, terrestrial isopods, water loss rate.

Introduction

Currently, terrestrial isopods are accepted as the only suborder of crustaceans in which almost all species (approximately 3600) (Schmalfuss, 2003) are completely free of the aquatic environment. Woodlice are successful land colonizers, as shown by their wide variety of colonized environments (from semi-aquatic to desert) and their cosmopolitan distribution (Vandel, 1960, 1962; Linsenmair, 1974; Warburg, 1993; Schmalfuss, 2003; Magrini *et al.*, 2010; Hornung, 2011). This success gives the unique lineage special importance for understanding the process of terrestrialization in arthropods.

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Woodlice exhibit physiological adaptations to terrestrial life that appear relatively weak compared with those of insects (Edney, 1977; Cloudsley-Thompson, 1988; Hornung, 2011). For example, woodlice do not have a waxy cuticle, making them extremely vulnerable to desiccation (Hadley & Quinlan, 1984; Gibbs & Rajpurohit, 2010). The water loss is primarily the result of passive cuticular evaporation (especially from the pleopods) and, to a much lesser extent, the activity of the excretory system and fluid discharges from the digestive tract (Edney, 1951; Lindqvist, 1972; Hadley & Quinlan, 1984; Carefoot, 1993; Wright & Machin, 1993; Greenaway & Warburg, 1998; Dias *et al.*, 2013).

To overcome this high dependence on water in terrestrial environments, woodlice have developed several behavioural strategies. The simplest strategy, which involves only the individual, is to be active at night. Woodlice forage during the night

(a cooler and wetter period than the daytime) and rest in dark and damp microhabitats during the day (Cloudsley-Thompson, 1956, 1959; Den Boer, 1961; Warburg, 1965; Carefoot *et al.*, 1998; Tuf & Jeřábková, 2008). In this way, each woodlouse limits its individual risk of desiccation. The second strategy involves the group. Indeed, woodlice are commonly gregarious (i.e. social aggregation) (Devigne *et al.*, 2011) and it is easy to observe many individuals aggregated in the same microhabitat during the day (Den Boer, 1961; Davis & Sutton, 1977; Hornung & Warburg, 1995, 1996; Hassall *et al.*, 2010). Note that terrestrial isopods may locate conspecifics via an aggregation pheromone (Kuenen & Nooteboom, 1963; Takeda, 1984). Aggregation reduces the body surface area exposed to the air (and, therefore, the surface sensitive to transpiration) for each individual (Allee, 1926), thereby contributing to a reduction of the high water loss rate. A dense aggregate may also create a local humid microclimate for all individuals in a small volume (Schliebe, 1988). As a result, for a woodlouse, the short-term survival of a dry period depends on the proximity of conspecifics in many circumstances (Allee, 1931; Takeda, 1984). This probably explains why aggregation is so frequently observed in woodlice, both in the field and in the laboratory; for other benefits of aggregation in woodlice, see also Broly *et al.* (2013).

Maintaining body water is a vital and chronic constraint for all terrestrial organisms. Aggregation, whether social or not, is most likely a mechanism for body water conservation in many invertebrate groups. Examples of this phenomenon are found in Mollusca (Cook, 1981; Chapman & Underwood, 1996; Rojas *et al.*, 2013); Tardigrada (Ivarsson & Jönsson, 2004); Acari (Glass *et al.*, 1998; Benoit *et al.*, 2007); Insecta, as in fly maggots (Rivers *et al.*, 2013), caterpillars (Klok & Chown, 1999, Schoombie *et al.*, 2013), beetles (Yoder *et al.*, 1992; Rasa, 1997; Yoder & Smith, 1997; Benoit *et al.*, 2005), crickets (Yoder *et al.*, 2002) and cockroaches (Yoder & Grojean, 1997; Dambach & Goehlen, 1999); and in certain semiterrestrial crabs (Yoder *et al.*, 2005). However, few of these studies have investigated the relationship between water losses and the size of the groups thoroughly; special attention has only been directed at small groups and at low density values.

The present study represents the first investigation of the rate of water loss in a wide range of group sizes in woodlice. For this, the common rough woodlouse *Porcellio scaber* Latreille is used; this terrestrial crustacean is well known for exhibiting widespread and large aggregations (Devigne *et al.*, 2011; Broly *et al.*, 2012). It is hypothesized that the loss of water is directly related to the surface area of the aggregates and varies in relation to both the density and the spatial arrangement of the aggregated individuals. Furthermore, the present study should allow a better understanding of the aggregation patterns and group sizes observed in woodlice, both in field and laboratory settings.

Materials and methods

Several hundred woodlice (*Porcellio scaber* Latreille 1804) were collected in the region of Lille (Northern France) and maintained in culture under the natural photoperiod of the region

(LD 16 : 8 h when the experiments were conducted in June), at $21 \pm 1.5\,°C$ and >80% relative humidity.

To test the relationship between the surface area of the aggregate and individual water losses, two set-ups were used. Set-up A was created to evaluate the water losses from the aggregates, and consisted of a Petri dish (diameter 9 cm) for which the lid was replaced by a fine mesh screen. First, groups of 1, 10, 20, 40, 60, 80 and 100 woodlice ($n = 10$ for each lot) were weighed once at the beginning of the experiment ($t = 0$). The groups were homogeneous: the weight of the groups increased linearly with the number of individuals (see the homogeneity control in the Supporting information, Figure S1, Doc. S1). The groups were then placed in the Petri dish for 1 h, after which they were again weighed to estimate the weight loss. The weights were determined using an Explorer E01140 balance (precision = 0.1 mg; Ohaus Corp., Parsippany, New Jersey). These experiments were conducted in a shaded room at $24 \pm 0.5\,°C$ and $40 \pm 1.5\%$ ambient humidity. In set-up B, which aimed to investigate the relationship between the number of individuals and the surface area of the aggregate, unpublished data obtained using the set-up previously described in Broly *et al.* (2012) were used. In these experiments, 10, 20, 40, 60, 80 or 100 woodlice were placed in a circular arena provided with shelters. The aggregation process was followed for 45 min, after which an image of the aggregates formed under the shelters was taken. The surface area of the aggregates was calculated by counting the number of pixels occupied by the aggregate (PHOTOSHOP, version 7.0.1; Adobe Systems Software, San Jose, California) and compared with the number of pixels occupied by the empty arena, whose surface area (cm^2) was known. The measurement of the area of the aggregate on the ground is a good approximation to the total surface area of the aggregate exposed to the air (see demonstration in the Supporting information, Doc. S1). The individual surface area is the total surface area of the aggregate divided by the number of individuals inside the aggregate.

Statistical analysis

Regression analyses were obtained using GRAPHPAD PRISM, version 5.01 (GraphPad Software Inc., La Jolla, California). The statistical tests were performed using GRAPHPAD INSTAT version 3.06 (GraphPad Software Inc.).

Results

The initial weight of an aggregate increases linearly according to the number of individuals in the aggregate (see Supporting information, Figure S1, Doc. S1). Therefore, the number of individuals and the initial weight both contributed significantly to the weight loss. Thus, it was difficult to determine which variable had the greatest impact because of their redundant effect on weight loss. As a result of these similarities, only results with the number of individuals in the aggregate on the horizontal axis are presented.

Figure 1(a) shows the mean weight loss (mg) of a woodlouse within an aggregate of 10, 20, 40, 60, 80 and 100 conspecifics and of an isolated individual after 1 h of exposure. The mean
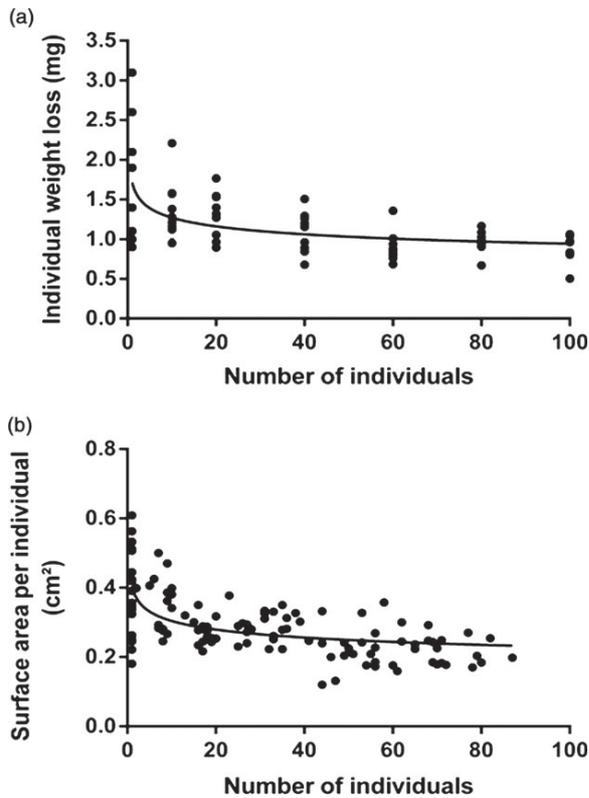
Fig. 1. (a) Individual weight loss (mg) in the aggregates of the wood-louse *Porcellio scaber* as a function of the number of individuals in the aggregate. The nonlinear regression for this dataset is indicated by the solid line. (b) The approximate individual surface area exposed to the air (cm^2) within aggregates of *P. scaber*, according to the number of individuals in the aggregate. The nonlinear regression for this dataset is indicated by the solid line.

weight loss of an individual decreases with the number of individuals in the aggregate according to the power function:

$$\text{Individual weight loss} = A \times \text{number}^B$$

where $A = 1.716$ [95% confidence interval (CI) = 1.504 to 1.0928], $B = -0.1304$ (95% CI = -0.1714 to -0.08933), d.f. = 68, $R^2 = 0.3447$.

An analysis using the initial weight of the aggregate on the horizontal axis showed the same pattern as Fig. 1(a). The mean proportion of weight loss decreases similarly with the initial weight of the aggregate, as a result of the linear relationship between the weight of the aggregate and the number of individuals inside. This relationship follows the power function:

$$\frac{\text{Total weight loss}}{\text{Initial weight}} = A' \times \text{initial weight}^B$$

where $A' = 25.38$ (95% CI = 23.55 to 27.21), $B' = -0.1705$ (95% CI = -0.2035 to -0.1375), d.f. = 68, $R^2 = 0.5734$.

The mean weight loss per individual (expressed in percent of initial fresh weight) is shown in the Supporting information

(Table S1, Doc. S1). As for Fig. 1(a), the results show a rapid decrease in weight loss for small aggregate sizes and a relative stability for more than 40–60 individuals. These results imply that woodlice in aggregates of 100 and 60 conspecifics lose similar amounts of weight (see Supporting information, Table S1, Doc. S1).

If the aggregate is approximated by an ellipsoidal cap (Fig. 2), the measured surface area of the aggregate on the ground is very similar to the external surface area of the aggregate (see demonstration in the Supporting information, Figures S2a, b, c and S3, Doc. S1). Figure 1(b) shows the decrease in the approximate body surface area exposed to the air of a woodlouse in an aggregate according to the size of the aggregate. As for individual weight loss (Fig. 1a and see Supporting information, Table S1, Doc. S1), these results show that adding individuals to small aggregates is very effective at decreasing the individual's exposure to the air. Beyond 40 or 60 individuals, however, adding additional individuals does not strongly decrease the exposed surface area of each individual: the mean decrease in the body surface area exposed to the air stabilizes at approximately 50% in large groups (Fig. 1b and see Supporting information, Table S2, Doc. S1).

These data on surface area can be fitted by the power law:

$$\text{Surface } (cm^2) /\text{individual} = A \times \text{number}^B$$

where $A = 0.4049$ (95% CI = 0.3748 to 0.4349), $B = -0.1239$ (95% CI = -0.1510 to -0.09669), d.f. = 115, $R^2 = 0.3960$.

Discussion

First, these results confirm that, under dry conditions, a wood-louse loses a large portion of its fresh weight in a short time (up to 4.5% in 1 h). Woodlice are known to release frequently various products such as gaseous ammonia (Wieser *et al.*, 1969; Wright & O'Donnell, 1995), although this substantial weight loss can only be explained by high water loss through evapotranspiration (Allee, 1926; Edney, 1951, 1977; Bursell, 1955; Hadley & Warburg, 1986; Greenaway & Warburg, 1998). Indeed, the cuticle of most woodlice is highly permeable to water flux (Mayes & Holdich, 1975) as a result of the low density of cuticular lipids (Hadley & Quinlan, 1984; Hadley & Warburg, 1986). This water loss is, most likely, a passive process (Dias *et al.*, 2013).

Clearly, not all species of woodlice have the same resistance to desiccation: this property depends strongly on the size of the animal and its physiological adaptations to terrestrial life (Edney, 1954; Hadley & Warburg, 1986; Greenaway & Warburg, 1998; Tsai *et al.*, 1998; Schmidt & Wägele, 2001; Csonka *et al.*, 2013; Dias *et al.*, 2013). *Porcellio scaber* (suborder: Oniscidea) is considered moderately resistant to desiccation, as its mesic habitat suggests (Edney, 1954). Gunn (1937) and others have estimated that the total weight loss per hour of an isolated *P. scaber* (at 20°C in dry air) is 4%, and the results of the present study are consistent with this estimate. To illustrate the striking contrast between this rate of weight loss and that found in insects, a cockroach loses approximately 0.15% of its
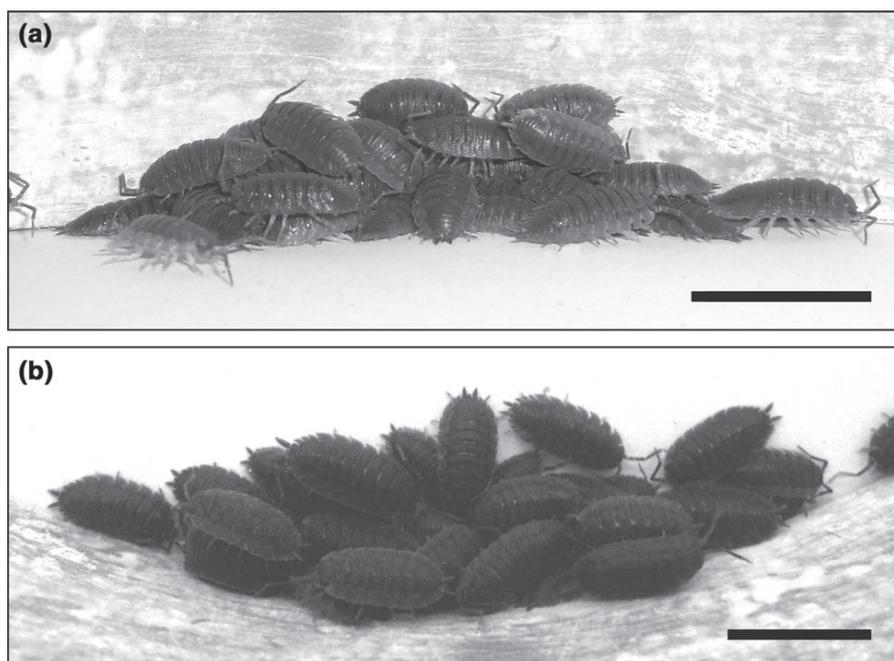
Fig. 2. Side (a) and top (b) views of an aggregate of the woodlouse *Porcellio scaber* comprising 40 woodlice. Scale bar = 1 cm.

fresh weight under the same conditions (Gunn, 1937; Edney, 1951; Yoder & Grojean, 1997). Because the lethal level of water loss in woodlice is approximately 40% (Dias *et al.*, 2013), isolated individuals can only survive for a few hours without water uptake (Allee, 1931; Takeda, 1984), unlike most insects (e.g. see the noteworthy survival duration of several days for cockroaches under drying conditions reported by Yoder & Grojean, 1997; Dambach & Goehlen, 1999). Therefore, it is evident that the regulation of the water balance is one of the most important factors in the life history of woodlice (Warburg, 1989). This strong water dependence certainly drives many of the distributional patterns and behaviours found in this taxon (Allee, 1926; Cloudsley-Thompson, 1956; White & Zar, 1968; Warburg, 1993; Csonka *et al.*, 2013; Dias *et al.*, 2013).

The results also show a clear relationship between the number of woodlice included in an aggregate (or the total weight of the aggregate) and the water losses of individuals. Based on this information, it is confirmed that aggregation reduces the water loss rate successfully because, whatever the size of the group, an isolated woodlouse loses more water than grouped individuals (Allee, 1926). Isolated woodlice lose approximately twice as much water as their counterparts in large aggregates with more than 40 woodlice. The important efficiency in the reduction of the water loss rate and the high sensitivity of individuals to desiccation most likely explains why the aggregation process is so rapid (Caubet *et al.*, 2008; Devigne *et al.*, 2011; Broly *et al.*, 2012) and why aggregation behaviour is so often observed in woodlice (Broly *et al.*, 2013).

However, because a power law describes the dynamic of the system, a member of an aggregate of 60 individuals does not lose more water (1.9%) than a member of an aggregate of 100 individuals (1.8%). Note that the individual water loss in large groups does not reach a plateau: it continues to decline, although very slowly, in contrast to the rapid decline of the water loss rate in small groups.

This relationship between individual water loss and the total number of aggregated individuals can be explained by the spatial arrangement of the aggregate. Individuals tend to form compact, cap-shaped piles. The individual surface area exposed to the air follows a power law ($x^{-0.12}$) dependent on the size of the aggregate. The water losses follow a similar power law ($x^{-0.13}$). Thus, the water losses in aggregated woodlice are most likely strongly determined by the geometrical arrangement of the individuals, which resembles an ellipsoidal cap. It is interesting to note that, in the studied aggregates of woodlice, the water losses and surface area exposed to the air tend to approach a value of a spherical conformation ($= x^{-0.33}$), the shape with the minimum surface/volume ratio. The deviation from a perfect spherical conformation can be explained by several geometrical, physical and physiological hypotheses. First, and quite obviously, the arrangement of individuals (inter-individual distance, number of layers in the aggregate, strong positive thigmotactic behaviour) could influence the efficiency with which aggregation can limit water loss limitation (e.g. see the effect of the clustered arrangement of butterfly eggs on the desiccation rate; Clark & Faeth, 1998). Moreover, woodlice do not lose water evenly. The ventral surface (pleopodal lungs) is the most sensitive (Edney, 1951).

As illustrated by the celebrated Bergmann's (1847) and Allen's (1877) rules for body heat loss, the relationship between the rate of water loss and individual size has long been known and comprises the subject of many studies (e.g. for woodlice: Dias *et al.*, 2013 or Tsai *et al.*, 1998). Furthermore, larger

individuals have lower rates of water loss (Tsai *et al.*, 1998; Dias *et al.*, 2013) because larger bodies have a proportionally smaller surface–volume ratio and, thus, a smaller surface area for exchange with the external environment. In the present study, an aggregate of *P. scaber* can be observed as a large entity composed of multiple subunits attempting to approach (collectively) an optimum form to limit desiccation for each subunit. The present study offers a new argument to support the importance of sociality and group effects in the successful occupation of terrestrial habitats by crustaceans (Yoder *et al.*, 2005; Broly *et al.*, 2013).

In these experiments, large groups are forced to form aggregates in small enclosed areas. However, extremely large groups are rarely observed under natural conditions [natural group sizes range from a few individuals (Cole, 1946) to approximately 50 individuals (Paris, 1963; Davis & Sutton, 1977) according to environmental conditions]. In laboratory experiments, aggregates of more 50 individuals are more frequent but seldom exceed 70 individuals (Broly *et al.*, 2012; P. Broly, unpublished observations). The results reported in the present study could explain these patterns. Based on considerations of water loss, a migrant has no more interest in entering an aggregate of 100 congeners than in entering an aggregate of 60. Even worse, it is probable that joining an overly large aggregation will produce more costs than benefits, especially in terms of foraging interference, sexual competition or disease transmission (Ganter, 1984; Dangerfield, 1989; Hassall & Dangerfield, 1990; Brockett & Hassall, 2005). Therefore, the collective decision-making observed in nature and in the laboratory, which produces groups of fewer than 50–60 individuals, is rational from an adaptive point of view.

In terrestrial isopods, there are many species less sensitive to desiccation than *P. scaber* and therefore better adapted to terrestrial life (Edney, 1968). These species present various physiological and/or morphological adaptations to limit desiccation. For example, species of the genus *Armadillidium* present a relatively round body (Vandel, 1962; Smigel & Gibbs, 2008) and have a thick cuticle (Csonka *et al.*, 2013). Interestingly, species that are better able to resist desiccation as individuals show a relatively moderate degree of aggregation behaviour compared with *P. scaber* (Hassall *et al.*, 2010). This example provides an excellent illustration of the trade-off between physio-morphological adaptations to terrestrial life and behavioural adaptations. It highlights the importance of a complete understanding of the driving forces leading to the evolution of sociality (Thiel, 2011). The comparative study of these key species deserves more attention.

Many unresolved issues remain, especially concerning the effect of aggregation at the individual level. The data reported in the present study represent the mean weight losses per individual calculated from the total weight loss of the aggregate. It is obvious that, at the individual level, woodlice gain various benefits that depend on their spatial position in the aggregate (Hamilton, 1971; Krause & Ruxton, 2002; Hirsch, 2007; Morrell & Romey, 2008). In particular, the woodlice at the centre of the aggregate are expected to gain more protection from desiccation than those at the periphery. In addition, individual desiccation resistance could vary according to the life stages of each individual (David & Vannier, 2001). Therefore, a more detailed analysis of water loss rates in identified individuals could lead to a better understanding of optimal strategies for group and collective decisions (e.g. compaction, dispersion and turnover).

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/phen.12060

Doc. S1. Additional data and mathematical demonstration.

Acknowledgements

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