COMPARATIVE WATER RELATIONS OF ARANEID AND LYCOSID SPIDERLINGS (ARACHNIDA)

FRED PUNZO and JOHN JELLIES

1Department of Biology, Division of Science and Mathematics, University of Tampa, Tampa, FL 33606 and
2Department of Biological Sciences, Illinois State University, Normal, IL 61761, USA

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Abstract—1. Second instars of Argiope aurantia and Lycosa avida were desiccated in moving air at relative humidities (r.h.) of 2, 33, 82 and 98%.
2. Initial rates of water loss were greater at higher humidities.
3. Rehydration did not result in any significant weight change but did cause a doubling of the initial rate of water loss when spiderlings were re-exposed to low r.h.
4. Under low r.h., these spiderlings exhibit cuticular permeabilities which resemble xeric arthropods, whereas under high r.h. the permeabilities are similar to mesic arthropods.
5. A possible mechanism for the regulation of water loss based on the physiochemical properties of the cuticle is described.

INTRODUCTION

Previous studies have demonstrated that the activity and distribution of terrestrial arthropods is influenced by the ability of the organism to compensate for evaporative water loss (see review by Edney, 1977). Several recent investigations have verified the relationships that exist between environmental conditions in which arthropods are found and their physiological adaptations (Cohen, 1982; Punzo & Mutchmor, 1980; Warburg et al., 1980). There have also been numerous studies on the comparative water relations of xeric vs mesic arthropods (Ahearn, 1970; Cohen & Cohen, 1981; Cohen et al., 1981; Humphreys, 1975; Jackson et al., 1980; McQueen, 1980; Punzo & Mutchmor, 1980; Vollmer & MacMahon, 1974). Generally, these studies have shown that rates of water loss are lower in xeric species and can be correlated with the rate of water movement across the cuticle. The cuticular permeability of arthropods from mesic habitats can be several orders of magnitude higher than that of xeric species (Anderson & Prestwich, 1982; Hadley, 1980; Jackson et al., 1980). Thus, cuticular permeability represents an evolutionary parameter closely related to environmental stress.

The problem of cuticular permeability is further intensified by small body size such as that found in mites (Arlian & Wharton, 1974; Edney, 1977) and ticks (Davis, 1974; McMullen et al., 1976; Megaw, 1974). To compensate for this, some species of mites and ticks have evolved mechanisms for absorbing water vapor (Arlian & Wharton, 1974). McMullen et al. (1976) reported on the uptake of water vapor by the salivary glands of ixodid ticks. A highly impermeable cuticle and/or an active mechanism for water uptake is clearly advantageous to small arachnids due to their large relative surface area.

Most of the previous research involving the water relations of spiders has focused on adult animals. Due to the paucity of data available for immature spiders and the important relationship that exists between small body size and rate of evaporative water loss, the present comparative study was undertaken in order to evaluate the dynamics of water loss in mesic araneid (Argiope aurantia) and lycosid (Lycosa avida) spiderlings.

MATERIALS AND METHODS

Egg sacks of the garden spider, Argiope aurantia, were collected from the roadside prairie in McLean Co., Illinois, during October, 1980, and maintained outdoors in a ventilated clear plastic box. Spiderlings of this species overwinter as second instars encased in dark egg sacs that are affixed to standing grasses approx. 30 cm above the ground. Spiderlings obtained from sacs with evidence of parasitism or other damage were not used in the study. The egg sacs were brought into the laboratory (22 C, 58% r.h.) three days prior to testing. Second instar Lycosa avida spiderlings were obtained from adult females maintained in the laboratory. Adult females were collected from grassy fields and leaf litter in Macoupin Co., II and maintained as described in a previous paper (Punzo, 1982). Voucher specimens have been deposited in the University of Tampa Invertebrate Collection.

Fifteen spiderlings of each species were placed individually in plastic cylinders (one group of 15 animals for each experimental condition). These cylinders were 2 cm long and 0.5 cm in diameter, and provided with silicone plugs at one end and polyester fiber plugs at the other end. Each cylinder was perforated with pin holes to allow for air circulation. Argiope spiderlings were transferred to the cylinders by pulling on the silk in the egg sac, dropping the animals onto a clean surface and allowing them to grasp the tip of a fine forceps. Lycosa spiderlings were dislodged from the parent female with a fine-hair brush and allowed to grasp the forceps. Spiderlings were then transferred from the forceps to the cylinders. Individual spiderlings were initially weighed on a Sauter balance to the nearest 0.005 mg, and re-weighed at 12-hr intervals for two days. As in previous studies (Cohen et al., 1981; Humphreys, 1980; Punzo & Mutchmor, 1980), water loss and weight loss were regarded as equivalent. Defecation was minimal.
Fig. 1. Diagrammatic representation of the desiccation apparatus used to recycle air at 3.8 l/min over *Argiope aurantia* and *Lycosa avida* spiderlings. Desired relative humidities were obtained with appropriate saturated salt solutions and silica gel.

The surface area of individual spiderlings was obtained using the relationship, \( S = kW^{2/3} \), where \( S \) represents the surface area in \( \text{cm}^2 \), \( W \) is the weight in mg, and \( k \) is a species-specific constant (Edney, 1977). The constant \( k \) was obtained by clearing spiders of known weight in KOH and spreading their exoskeletons on paper provided with 0.25 mm squares as described by Wharton et al. (1980). The exoskeletons were then measured under a dissecting microscope. The values arrived at for \( k \) were 0.128 \( \text{cm}^2/\text{mg} \) for *A. aurantia*, and 0.131 \( \text{cm}^2/\text{mg} \) for *L. avida*.

A procedure similar to that reported by Punzo & Mutchmor (1980) and Wilson et al. (1982) was used to evaluate the effect of r.h. on cuticular permeability. Partially desiccated animals from the 33\% r.h. group were exposed to 98\% r.h. conditions and weights were determined at 12-hr intervals for two days. The spiderlings were then re-introduced to the 33\% r.h. regime and weighed after 24 hr. The temperature (25°C) was kept constant during these experiments since temperature has been shown to alter cuticular structure in arthropods (Davis, 1974; Edney, 1977; Hadley, 1980; Riddle, 1981).

Results have been listed in tabular form or plotted using Student t-test values with 95\% confidence intervals. Saturation deficit was calculated according to the procedure described by Hill (1976).

### Results

The results listed in Table 1 show the effects of dry air on *A. aurantia* and *L. avida* spiderlings. Under dry air conditions (2 and 33\% r.h.), both of these mesic species exhibited cuticular permeabilities that compare favorably with those reported for xeric arachnids (Cohen & Cohen, 1981; Jackson et al., 1980; Vollmer & MacMahon, 1974; Warburg et al., 1980). Under high humidity conditions (82 and 98\% r.h.), these spiderlings exhibited cuticular permeabilities that resemble those reported for mesic arachnids (Cohen, 1982; Edney, 1977; Hadley et al., 1981). Thus, at high r.h. (Table 1), the cuticular permeabilities of *A. aurantia* and *L. avida* was approx. 38 times greater than the permeabilities exhibited at low r.h. In addition, Fig. 2 and Table 2 show that weight loss within the first 12 hr was greater at high r.h. No significant difference was found between these two species. These results indicate that cuticular permeability becomes more linear as the saturation deficit increases. However, it can be seen that saturation deficit appears to be inversely related to permeability. Careful observation of the data shown in Fig. 3 and Table 3 shows that the rates of water loss rapidly decelerate after the initial loss. This is in general agreement with data reported for other terrestrial arthropods (Edney, 1977) and suggests that the rate of evaporative water loss is a prop-

![Diagram of desiccation apparatus](image-url)
Comparative water relations of araneid and lycosid spiderlings

Fig. 2. Mean weight loss for Argyrope aurantia spiderlings desiccated at four relative humidities over a period of 48 hr. Data points represent $X \pm 0.95$ confidence interval. $N = 15$.

The results listed in Table 4 show the effects of desiccation and rehydration on these spiderlings. When both species were partially dehydrated (at 33% r.h.) for 48 hr, there was a pronounced weight loss. Following a subsequent 48 hr exposure to high (98% r.h.) conditions, their weights remained relatively constant. Subsequent re-exposure for 24 hr at the lower r.h. (33%) resulted in an additional weight loss.

Table 2. Mean weight loss ($\text{mg/cm}^2$) for Lycosa arida spiderlings desiccated at four relative humidities over a period of 48 hr. $N = 15$

<table>
<thead>
<tr>
<th>Period of exposure (hr)</th>
<th>2</th>
<th>33</th>
<th>82</th>
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</thead>
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<tr>
<td>12</td>
<td>0.24</td>
<td>0.30</td>
<td>0.42</td>
<td>0.53</td>
</tr>
<tr>
<td>24</td>
<td>0.49</td>
<td>0.42</td>
<td>0.47</td>
<td>0.59</td>
</tr>
<tr>
<td>36</td>
<td>0.80</td>
<td>0.74</td>
<td>0.60</td>
<td>0.79</td>
</tr>
<tr>
<td>48</td>
<td>1.04</td>
<td>0.81</td>
<td>0.83</td>
<td>0.86</td>
</tr>
</tbody>
</table>

Table 3. Mean weight loss ($\text{mg/cm}^2$/hr $\times 10$) for Lycosa arida spiderlings as a function of relative humidity and period of exposure. $N = 15$

<table>
<thead>
<tr>
<th>Period of exposure (hr)</th>
<th>2</th>
<th>33</th>
<th>82</th>
<th>98</th>
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<tr>
<td>12</td>
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<td>0.27</td>
<td>0.40</td>
<td>0.45</td>
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<tr>
<td>24</td>
<td>0.24</td>
<td>0.21</td>
<td>0.23</td>
<td>0.23</td>
</tr>
<tr>
<td>36</td>
<td>0.21</td>
<td>0.21</td>
<td>0.18</td>
<td>0.20</td>
</tr>
<tr>
<td>48</td>
<td>0.19</td>
<td>0.20</td>
<td>0.19</td>
<td>0.16</td>
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</table>

Table 4. Mean weight loss (mg/cm$^2$) for desiccated Argyrope aurantia and Lycosa arida spiderlings exposed to low r.h. (33%) for 48 hr, to high r.h. (98%) for the next 48 hr, and then re-exposed to low r.h. (33%) for 24 hr. $N = 15$

<table>
<thead>
<tr>
<th>Period of exposure (hr)</th>
<th>Relative humidity (%)</th>
<th>Argyrope aurantia</th>
<th>Lycosa arida</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>33</td>
<td>0.22</td>
<td>0.24</td>
</tr>
<tr>
<td>24</td>
<td>33</td>
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<td>36</td>
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</tr>
<tr>
<td>60</td>
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<td>0.82</td>
</tr>
<tr>
<td>72</td>
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</tr>
<tr>
<td>84</td>
<td>33</td>
<td>0.82</td>
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</tr>
<tr>
<td>96</td>
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<td>0.81</td>
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<tr>
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<td>1.51</td>
<td>1.59</td>
</tr>
<tr>
<td>120</td>
<td>33</td>
<td>2.06</td>
<td>2.24</td>
</tr>
</tbody>
</table>

Fig. 3. Mean acceleration curves for weight loss in Argyrope aurantia spiderlings. Open circles represent 2% r.h.; closed circles (33% r.h.); closed triangles (82% r.h.); open triangles (98% r.h.). Data points represent the mean $+0.95$ confidence interval. $N = 15$.

The rate of water loss upon re-exposure to 33% r.h. (Table 4) is approximately twice that found for the 98% exposure period for both species. No significant differences were found between the desiccation and rehydration responses of these two species.

DISCUSSION

The results of the present study strongly suggest that r.h. per se can exert an influence on rate of water loss, presumably by affecting the permeability characteristics of the cuticle. Loveridge (1968) showed that the insect, Locusta migratoria, is capable of responding to low humidity conditions by closing the spiracles. This explanation does not seem to apply to
the A. aurantia and L. arida spiderlings tested in this study since dehydrated animals did not appear to open their respiratory passages under high humidity (Table 4). That is, their weights remained relatively constant, and dropped only after being re-exposed to lower r.h. It is reasonable to assume that these spiderlings, like other terrestrial arthropods (Edney, 1977; Punzo & Mutchmor, 1980), would not open their spiracles in response to a low humidity regime. Thus, the respiratory passages of these spiderlings are probably closed or non-functional. In view of this, these spiderlings represent an excellent system for evaluating cuticular water loss in the absence of other possible complicating factors.

The effects of r.h. on cuticular permeability (weight loss) indicate that water loss is initially greater under high humidity regimes for these species (Table 1). The results shown in Tables 2, 3, and 4, and Figs 2 and 3 further suggest that water loss through the cuticle is effected by humidity directly. Hadley et al. (1981) reported similar results for the troglobitic spider, Lycosa howarthi but found water loss rates to be independent of r.h. in an undescribed epigean spider, Lycosa sp. Rates of water loss through the cuticle of terrestrial arthropods have been shown to be influenced by r.h. in the whipscorpion Mastigoproctus giganteus (Ahearn, 1970), the mite Dermatophagoides farinae (Arlian & Wharton, 1974), several species of ticks (Davis, 1974; McMullen et al., 1976; Megaw, 1974), isopods (Edney, 1977), stored-product insects (Punzo & Mutchmor, 1980), desert cockroaches (Cohen & Cohen, 1981), desert beetles (Cohen et al., 1981; Jackson et al., 1980; Wilson et al., 1982), scorpions (Warburg et al., 1980), and several species of adult spiders (Humphreys, 1973; Seymour & Vinegar, 1973; Vollmer & MacMahon, 1974).

Berridge (1970) postulated several possible barriers to water loss by the cuticle. One involves an active pumping mechanism whereby water is transported against a vapor pressure gradient back into the body. This would result in the net uptake of water when partially desiccated animals are subjected to high r.h. conditions. Another barrier to water loss resides in the chemical composition (waxes and lipids) of the epicuticle. The water-proofing nature of this epicuticle layer of the cuticle is well known among the insects and arachnids (Berridge, 1970; Edney, 1977; Hadley, 1980). A third major barrier to water loss could reside in the apical membrane of the epidermal layer which underlies the cuticle proper. There is evidence that the apical membrane plays a role in restricting water loss in adult scorpions and beetles (Riddle, 1981). The results of the present study indicate that A. aurantia and L. arida spiderlings probably do not possess an active pumping mechanism as described above to restrict water loss. If such a pump were present, one would expect these animals to gain weight shortly after being desiccated and then exposed to a high r.h. This was not the result found in this study (Table 4). With respect to the epicuticle, although these spiderlings exhibit an adult-like pigmentation, the rapid rate of water loss exhibited under high r.h. conditions suggests that it is not an effective barrier to water loss. Perhaps the degree of sclerotization in these spiderlings is not as complete as it is in adults.

The cuticle of arthropods is a complex laminar matrix composed primarily of chitin and protein and is highly hygroscopic (Hackman, 1971). In view of this, the results of the present study may be attributed to the fact that the degree of hydration of this matrix profoundly influences its permeability to water (Berridge, 1970; Hadley, 1980). Under conditions of high r.h. the endocuticle would approach an equilibrium with body fluids. A small saturation deficit would take longer to dehydrate the hydrated cuticle than would a larger deficit. Thus, while the cuticle remains hydrated, total body water loss is accelerated while under low r.h. (high saturation deficit); the cuticle becomes dehydrated and thus opposes water loss (Fig. 2, Table 2). Since water loss under all r.h. values is of the same absolute magnitude, these rates of water loss most likely reflect a physical property of the cuticle. It appears that saturation deficit tends to dehydrate these spiderlings but the presence of a vapor pressure gradient is qualitative, not quantitative. That is, over time, these animals will lose the same absolute amounts of water as long as a gradient exists regardless of the magnitude of the gradient. Similar experiments on ticks did not yield the same results (Hafez et al., 1970). It must be pointed out however, that the ticks were subjected to an intermediate r.h. (60%) before water loss was evaluated after a subsequent re-exposure to a lower r.h. The results of the present study (Figs 2 and 3, Table 4) indicate that water loss at such an intermediate r.h. would probably be rapid enough to approach the cuticle specific rate (Edney, 1977) and then decrease at the same rate that was initially observed under low r.h. conditions.

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