Weather and the use of empty gastropod shells by arthropods

GREGORIO MORENO-RUEDA (1,2), CARLOS MARFIL-DAZA (3), F. JAVIER ORTIZ-SÁNCHEZ (4) & ANTONIO MELIC (5)

(1) Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Österreichische Akademie der Wissenschaften, Savoyenstraße 1a, A-1160, Wien, Austria
(2) Departamento de Biología Animal, Facultad de Ciencias, Universidad de Granada, E-18071, Granada, Spain
(3) Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Pabellón del Perú, Avda. María Luisa, s/n, E-41013 Sevilla, Spain
(4) Grupo de Investigación “Transferencia de I+D en el Área de Recursos Naturales”, Universidad de Almería, Ctra. de Sacramento, s/n, E-04120 La Cañada de San Urbano, Almería, Spain
(5) Sociedad Entomológica Aragonesa (S.E.A.), Avda. Radio Juventud 37, E-50012, Zaragoza, Spain

Abstract. Arthropods frequently use empty snail shells as shelter or nesting sites. This study analyses the use of shells from the arid-dwelling land snail *Sphincterochila candidissima* (Draparnaud 1801) by arthropods in the Sierra Elvira (south-eastern Spain). Arthropods of 11 different orders occupied 15.6% of shells. Salticidae (54.6%) and Apoidea (21.3%) comprised the majority of arthropods. Shells were used primarily when environmental temperatures were lowest, suggesting that, in the Sierra Elvira, arthropods use shells to escape from the cold. Weather explained 73% of the variation in shell occupation. However, Apoidea used shells independently of weather, occupying shells as nesting chambers. These results suggest that snail shells may be important refugia and nesting sites for arthropod fauna.


Keywords: *Sphincterochila*, snail, Spain, Salticidae, Apoidea.

Arid and semi-arid environments, with scarce availability of water and high temperatures, offer restrictive living conditions for organisms. High temperatures may negatively affect organisms such as arthropods (Holm & Edney 1973), and individuals that use more effective thermal refugia (for them and/or their offspring) are more likely to survive and reproduce in these environments. Potential refugia for many arthropods include empty snail shells (Szinetar *et al.* 1998; Gess & Gess 1999). Although snails are highly sensitive to desiccation (Prior 1985), several species dwell in arid and semi-arid environments (Arad *et al.* 1989). To minimize water losses, snails have a number of different strategies, such as light-coloured shells to reduce radiation absorption and thereby reduce heat (Schmidt-Nielsen *et al.* 1971). These adaptations frequently make snail shells ideal refuges for arthropods and their clutches.

Gastropod shells can provide both adult arthropods and their clutches refuge against predators (e.g., Tricarico & Gherardi 2006). Arthropods, due to their cuticle structure, are in general quite heat-resistant, however they are more sensitive to low temperatures (Wehner *et al.* 1992). Gess & Gess (1999) described the use of empty shells by arthropods in the desert of Namibia, primarily as shelter and nesting sites. This behaviour might help arthropods avoid heat in arid environments. If so, we would expect shells to be more frequently used by arthropods when the risk of thermal shock is higher.

In the present work, we analyse the use of *Sphincterochila candidissima* (Draparnaud 1801)
snail shells by arthropods in the Sierra Elvira (south-eastern Spain). *Sphincterochila candidissima* is a typical, arid-adapted snail, and has a thick-walled, narrow-apertured, white shell. All of these shell characteristics probably serve to maintain a cool microclimate within the shell (Moreno-Rueda 2002, 2007). This snail inhabits the Sierra Elvira, a small mountain range within the mesomediterranean dry climate (UNESCO 1963). The climate of the study area is harsh and dry, experiencing up to 5 months of drought (Alonso et al. 1985). We studied the seasonal use of snail shells by arthropods, as well as the relationship between shell use and weather. Our ultimate goal is to describe and quantify the use of shells by arthropods, and to understand the causes of shell use.

### Material and Methods

The work was carried out from October 2004 through September 2005 in the Sierra Elvira (SE Spain, 37° 15’ N, 3° 40’ W). The study was conducted on three plots, situated 100 m apart. Plot A had a substrate of bare soil, and vegetation consisted predominantly of rosemary (*Rosmarinus officinalis* L.). Plot B was in rocky with scarce vegetation, and also dominated by rosemary. Plot C had a substrate of limestone and bare soil, and vegetation consisted of rosemary and grasses. Once a month (around the 15th), 100 shells of dead *Sphincterochila candidissima* were collected in each plot (300 shells per month in total). Each shell was individually placed in a plastic bag, which was immediately sealed, meanwhile checking carefully whether any occupant left the shell. In the laboratory, the shells were opened and their contents checked. Arthropods found in the shells were identified, at minimum, to order, and then preserved in ethanol 96%.

Weather data were taken from the Pinos Puente weather station (web of the Consejería de Agricultura y Pesca, Junta de Andalucía), situated near the study area. The variables taken each month included: minimum, maximum, and mean temperature (°C); minimum, maximum, and mean relative humidity (%); wind speed (m/s); rain (mm); mean daily solar radiation (MJ/m²); and mean daily evapotranspiration (mm). All weather variables displayed approximately normal distributions according to Kolmogorov-Smirnov tests, so we used parametric statistics. Weather variables were highly correlated (correlation index in absolute value between 0.99 and 0.71, except with the rain: 0.31 < |r| < 0.75). This suggests that the use of all weather variables in multivarient analyses could show multicollinearity (Quinn & Keough 2006). For this reason, the number of variables was reduced using Principal Components Analysis (PCA). The first PCA axis explained the 85.3% of the variance, while the factor 2 explained only a 7.7%. Factor 1 (PC1) was positively correlated with temperature, radiation, wind, and evapotranspiration (Table 1), and negatively correlated with relative humidity and rain, resulting in a positive index for temperature and a negative index for humidity.

### Table 1. Correlations between every weather variable and PCA factors 1 and 2.

<table>
<thead>
<tr>
<th>Factor 1</th>
<th>Factor 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (maximum)</td>
<td>0.976</td>
</tr>
<tr>
<td>Temperature (minimum)</td>
<td>0.928</td>
</tr>
<tr>
<td>Temperature (mean)</td>
<td>0.962</td>
</tr>
<tr>
<td>Relative humidity (maximum)</td>
<td>–0.974</td>
</tr>
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<td>Relative humidity (minimum)</td>
<td>–0.923</td>
</tr>
<tr>
<td>Relative humidity (mean)</td>
<td>–0.976</td>
</tr>
<tr>
<td>Wind</td>
<td>0.818</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>0.965</td>
</tr>
<tr>
<td>Precipitation</td>
<td>–0.685</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>0.986</td>
</tr>
</tbody>
</table>

### Table 2. Number of specimens of every Arthropod order found in shells during the study period, and the total number of shells inspected.

* Salticidae and Apoidea data are indicated within their respective orders; and 1 signifies larvae only.

<table>
<thead>
<tr>
<th>Month</th>
<th>X</th>
<th>XI</th>
<th>XII</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
<th>VIII</th>
<th>IX</th>
<th>Total</th>
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<tbody>
<tr>
<td>Araneae</td>
<td>16</td>
<td>63</td>
<td>46</td>
<td>44</td>
<td>32</td>
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<td>16</td>
<td>12</td>
<td>9</td>
<td>7</td>
<td>35</td>
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<td></td>
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<tr>
<td>* Salticidae</td>
<td>16</td>
<td>54</td>
<td>42</td>
<td>44</td>
<td>32</td>
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<td>26</td>
<td>14</td>
<td>12</td>
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<td>6</td>
<td>35</td>
<td>313</td>
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<tr>
<td>Hymenoptera</td>
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<td>13</td>
<td>11</td>
<td>9</td>
<td>14</td>
<td>14</td>
<td>12</td>
<td>10</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>158</td>
<td></td>
</tr>
<tr>
<td>* Apoidea</td>
<td>11</td>
<td>7</td>
<td>5</td>
<td>5</td>
<td>10</td>
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<td>29</td>
<td>16</td>
<td>10</td>
<td>6</td>
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<tr>
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<td>1</td>
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</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td>1</td>
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<tr>
<td>Not occupied</td>
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<td>214</td>
<td>225</td>
<td>240</td>
<td>235</td>
<td>254</td>
<td>245</td>
<td>264</td>
<td>275</td>
<td>282</td>
<td>283</td>
<td>252</td>
<td>2992</td>
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<td>299</td>
<td>298</td>
<td>300</td>
<td>300</td>
<td>299</td>
<td>3543</td>
</tr>
</tbody>
</table>
Results

Shell occupancy

In total, 3543 shells were analysed (57 shells were lost), 551 of those (15.6%) were occupied by at least one arthropod. Arthropods located inside shells belonged to 11 different orders (Table 2). However, most arthropods belonged to the Salticidae family (54.6% of the specimens) or to the Apoidea superfamily (21.3%). Most Salticidae were *Pellenes nigrociliatus* (L. Koch 1875) (91.1%), usually adults, but sometimes accompanied by their clutches or spiderlings. Other Salticidae included *Salticus propinquus* Lucas 1846 (7.7%) and *Aelurillus aeruginosus* (Simon 1871) (1.2%). Besides Salticidae, other Araneae families found in shells included Clubionidae, Gnaphosidae, Zodariidae, Miturgidae, Theridiidae, Filistatidae and Thomisidae, each represented by one or two specimens, except *Haplodrassus* sp. (family Gnaphosidae), represented by 8 specimens.

Most Apoidea found in shells were developing specimens (larvae, pupae or individuals already formed that had not yet left the nest), and were still within breeding cells. Thirty nine individuals (24.7% of Hymenoptera) could not be identified because they were larvae or young pupae. The most frequent Apoidea species was *Rhodanthidium sticticum* (Fabricius 1793) (40.2% of Apoidea), followed by *Hoplosmia fallax* (Pérez 1895) (27.9%), *Osmia ferruginea* (Latreille 1811) (17.2%), and *Stelis odontopyga* Noskiewicz 1926 (6.6%), all they belonging to the family Megachilidae. Moreover, we found a few individuals of *Osmia versicolor* (Fabricius 1793) (2), *Protosmia glutinosa* (Giraud 1871) (3) and unidentified Apoidea (4).

Differences between plots

We found significant differences among plots in the frequency of shells used by the arthropods (*χ²* = 10.09; *p* < 0.01). The frequency of shells used was highest in plot A (18.2%; *n* = 1146), intermediate in plot C (15.2%; *n* = 1199), and lowest in plot B (13.4%; *n* = 1198). Differences among plots were caused by the percentage of shells occupied by Salticidae, which differed among plots (*χ²* = 19.23; *p* < 0.001; plots A: 11.0%, B: 6.0%, and C: 9.5%). In the case of Apoidea, and for all other groups, differences between plots were not significant (*χ²* < 5.0; *p* > 0.10 in both cases). In the remaining analyses, we verified that the patterns studied were similar in the three plots.

Seasonal variation

Frequency of shell use in the three study plots differed significantly among months (always *χ²* > 50.0; *p* < 0.001). This pattern did not differ significantly among plots across months (*χ²* = 31.61; *p* = 0.08), and therefore data from all three plots could be grouped. When the entire study area was considered, we found that the frequency of occupied shells differed significantly among months (*χ²* = 138.0; *p* < 0.001; Fig. 1). The percentage of occupied shells was highest in autumn-winter (November-February), when occupancy surpassed 20%, and lowest (<10%) during summer months (June-August) (Fig. 1).

Occupation by Salticidae differed significantly between months and followed the general pattern (*χ²* = 106.4; *p* < 0.001; Table 2; Fig. 2). Meanwhile, in Apoidea, differences among months in occupation frequency were significant (*χ²* = 49.1; *p* < 0.001), but exhibited a different pattern, with a higher shell occupation rate during spring months (Table 2; Fig. 2), probably because Apoidea look for snail shells not only for protection but also for nesting.
The occupation rate of Salticidae was negatively correlated with temperature, wind speed, solar radiation, and evapotranspiration, and positively correlated with relative humidity. However, shell occupation was not significantly correlated with rain (Table 3). Factor 1 (PC1) was negatively correlated with occupation rate (Table 3; Fig. 1), suggesting that arthropods used shells more when temperatures were lower and humidity was higher. This variable (PC1) explained 73.3% of the variance in occupation rate (Simple Linear Regression: $R^2 = 0.73$; $F_{1,10} = 27.5, p < 0.001$).

The occupation rate of Salticidae was negatively correlated with temperature, wind speed, solar radiation, and evapotranspiration, and positively correlated with relative humidity (Table 3). The percentage of shells occupied by Salticidae covaried negatively with PCA Factor 1 (Table 3; Fig. 2), implying that shells were used when temperatures were lower and humidity was higher. Factor 1 explained 64.2% of the variation in occupation rate by Salticidae (Simple Linear Regression: $R^2 = 0.64$; $F_{1,10} = 17.9, p < 0.002$). There was a similar tendency by all other arthropods (excluding Apoidea) (Table 3). On the contrary, weather did not explain seasonal variation in shell occupation by Apoidea (Table 3; Fig. 2).

**Discussion**

Our data show that arthropods use empty shells of the snail *Sphincterochila candidissima* as refugia and nesting sites in a semi-arid environment. Similar results were found by Gess & Gess (1999) in the desert of Namibia. Our work quantifies that most arthropods occupying shells in the Sierra Elvira are Salticidae and Apoidea.

Salticidae primarily used shells as refugia and nesting sites (also see Bauchhenss 1995; Bellmann 1997; Szinetar *et al.* 1998). Presumably, many other arthropods found within shells, such as Heteroptera or Diptera, also used them as refugia, although the case of Salticidae, especially *Pellenes nigrociliatus*, were observed with exceptional frequency. This species nests inside snail shells, and female spiders remain with their clutches and spiderlings, providing a measure of parental care (Mikulska 1961; Bellmann 1997). In fact, we frequently found adult females associated with offspring during spring samples. Shells also appeared to be used by the Salticidae and other arthropods (except the Apoidea) as shelters against low temperatures. Arthropods can be very resistant to heat, but not to cold (Wehner *et al.* 1997), and thus it is possible that high temperatures in the Sierra Elvira do not threaten the survival of these organisms, but winter low temperatures could. We consider unlikely that changes in occupancy merely reflect seasonal patterns of arthropod abundance; in fact, arthropod abundance at the study site is lower in winter (pers. obs.).

The pattern of shell use by Apoidea was different; shells were used exclusively for breeding, resulting in a greater use in spring. Hymenoptera frequently use empty shells to reproduce (O’Toole & Raw 1991; Bellmann 1995; Gess & Gess 1999). In this case, it is possible that shells offer cool microclimates that increase survival during the summer, protecting against desiccation, and affording protection against predators. As Gess & Gess (1999) reported, we also found some parasites, such as *Chrysura refulgens* (Spinola, 1806) (family Chrysididae, included within Hymenoptera), a potential parasite of Apoidea nests, with which they are associated (Mingo 1994). Cleptoparasitic Apoidea, belonging to the family Megachilidae (genus *Stelis* Panzer 1806), were also collected in the shells, and their presence indicates the maturity of the community of Apoidea (Ortiz-Sánchez *et al.* 2006).

There were between-plots differences in shell use by arthropods. These may have been due to variations in Salticidae abundance. Another possibility is that plots with lower shell occupancies contained alternative refugia. Shells were less used in plots with rockier substrates. Limestone rocks, through karstic erosion, contained hollows and cracks that could serve as refugia for arthropods.

### Table 3. Pearson product-moment correlation indices between arthropod shell use frequency (total, by Salticidae, by Apoidea, and by other arthropods) and weather variables measured.

<table>
<thead>
<tr>
<th></th>
<th>Total</th>
<th>Salticidae</th>
<th>Apoidea</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(maximum)</td>
<td>$-0.86^{**}$</td>
<td>$-0.78^{**}$</td>
<td>$-0.08^{ns}$</td>
<td>$-0.73^{**}$</td>
</tr>
<tr>
<td>(minimum)</td>
<td>$-0.84^{**}$</td>
<td>$-0.79^{**}$</td>
<td>$-0.05^{ns}$</td>
<td>$-0.70^{*}$</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mean)</td>
<td>$-0.86^{**}$</td>
<td>$-0.80^{**}$</td>
<td>$-0.05^{ns}$</td>
<td>$-0.72^{**}$</td>
</tr>
<tr>
<td>Relative humidity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(maximum)</td>
<td>$0.84^{**}$</td>
<td>$0.78^{**}$</td>
<td>$0.09^{ns}$</td>
<td>$0.67^{*}$</td>
</tr>
<tr>
<td>(minimum)</td>
<td>$0.75^{**}$</td>
<td>$0.65^{**}$</td>
<td>$0.05^{ns}$</td>
<td>$0.70^{*}$</td>
</tr>
<tr>
<td>Relative humidity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mean)</td>
<td>$0.80^{**}$</td>
<td>$0.75^{**}$</td>
<td>$-0.00^{ns}$</td>
<td>$0.71^{**}$</td>
</tr>
<tr>
<td>Wind</td>
<td>$-0.81^{***}$</td>
<td>$-0.87^{***}$</td>
<td>$0.38^{ns}$</td>
<td>$-0.80^{**}$</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>$-0.79^{**}$</td>
<td>$-0.78^{**}$</td>
<td>$0.19^{ns}$</td>
<td>$-0.74^{**}$</td>
</tr>
<tr>
<td>Precipitation</td>
<td>$0.45^{ns}$</td>
<td>$0.28^{ns}$</td>
<td>$0.02^{ns}$</td>
<td>$0.60^{***}$</td>
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<tr>
<td>Evapotranspiration</td>
<td>$-0.86^{**}$</td>
<td>$-0.84^{**}$</td>
<td>$0.08^{ns}$</td>
<td>$-0.75^{**}$</td>
</tr>
<tr>
<td>PCA1</td>
<td>$-0.86^{**}$</td>
<td>$-0.80^{**}$</td>
<td>$0.03^{ns}$</td>
<td>$-0.77^{**}$</td>
</tr>
</tbody>
</table>

Note: **p < 0.05; ***p < 0.001; ns not significant; $p < 0.01$; $p < 0.001$. 

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Finally, the relationship found between arthropods and the presence of *Sphincterochila candidissima* snails could have implications for arthropod conservation. Conservation of this snail may be important for the conservation of refugia and nest-building sites for arthropods, especially Salticidae and Apoidea. The implications of these relationships may extend throughout the trophic network. The facilitation of Salticidae would affect their prey species. Likewise, by favouring the reproduction of Apoidea (the principal group of pollinating hymenopterans), it is possible that *Sphincterochila candidissima* indirectly influences plant reproduction. For example, *Rhodanthidium sticticum*, the primary solitary bee nesting in *Sphincterochila candidissima* shells, is crucial for the reproduction of endemic plants such as *Antirrhinum microphyllum* Rothm. (Torres et al. 2002), and *Osmia versicolor*, the second in number, belongs to a bee genus commonly used for the pollination of cultivated plants (Bosch & Kemp 2002). Therefore, even after death, snail abundance may influence the reproduction and survival of diverse arthropods, and indirectly impact the ecosystem in Mediterranean regions.

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References


