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Refuge selection by two sympatric species of arid-dwelling land snails: Different adaptive strategies to achieve the same objective

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Abstract

Terrestrial gastropods, especially those dwelling in dry habitats such as the Mediterranean, are highly susceptible to dehydration. In this study, the use of refuges by *Iberus gualtieranus gualtieranus* and *Sphincterochila candidissima* is compared. These two species belong to families with different distribution ranges, but they live in sympatry on a mountain in southern Spain with a dry Mediterranean climate. *I. g. gualtieranus* used mainly rock crevices as refuges, consistently throughout the year. *S. candidissima* hibernated beneath humus during autumn and winter (*I. g. gualtieranus* did not hibernate). In spring, *S. candidissima* seemed active, while *I. g. gualtieranus* was already aestivating. In summer, *S. candidissima* aestivated on vegetation, while *I. gualtieranus* aestivated deep within crevices. These differences in the use of refuges may be explained on the basis of the need for more protection by *I. g. gualtieranus* because of its morphology, which is less suited to the dry habitat, but has evolved to enable this species to exploit karstic crevices as refuges more efficiently. These results illustrate that behaviour and morphology interact allowing both species to coexist in sympatry in an arid environment using different adaptive strategies.
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Keywords: Seasonal cycle; Morphology; *Iberus g. gualtieranus*; *Sphincterochila candidissima*; Microhabitat

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1. Introduction

Dry environments, usually having high temperatures, low moisture and scarce vegetation impose very restrictive living conditions on animals, which are especially critical for hydrophilic animals (Pianka, 2000). Terrestrial gastropods, having permeable skin and moving by laying down moist mucus trails, suffer high rates of dehydration (Prior, 1985; Luchtel and Deyrup-Olsen, 2001), and thus their distribution is affected by moisture, with more species and individuals in moister zones (Tattersfield, 1990; Wardhaugh, 1995; Ports, 1996). Nevertheless, some snails dwell in arid zones, where they must employ behavioural, physiological and/or morphological adaptations to minimise the risk of dehydration. For example, the species of the genus *Sphincterochila* lose mass by dehydration at different rates, those from drier environments losing water more slowly (Arad et al., 1989).

It might therefore be assumed that in dry environments the risk of dehydration is one of the primary selective forces acting on gastropods. Because snails in these environments are under similar selective forces, we might expect these species to evolve similar traits against dehydration (evolutionary convergence; Pianka, 2000). However, it is difficult to predict the evolution of populations of two different species with similar ecology in a given environment, as different solutions can resolve the same problem (Partridge and Harvey, 1988). The evolutionary route followed by a species depends on the initial evolutionary and phylogenetic constraints, and when certain traits have already evolved, it may be easier for a species to take one evolutionary path than another (McKitrick, 1993; Bennett and Owens, 2002). The result is that ecologically similar species may exhibit different traits in the same environment.

In this study, I compare the refuge selection in two species of gastropods, *Sphincterochila candidissima* and *Iberus gualtieranus*, that inhabit in sympatry in the Sierra Elvira. This is a mountain with a climate classified as accentuated mesomediterranean (UNESCO, 1963), with 5 months of drought in the study area (Alonso et al., 1985; see Fig. 1), thus a harsh environment for animals as hydrophilic as snails. In Sierra Elvira, *S. candidissima* and *I. gualtieranus* are the two dominant species, with similar densities, and are not found in

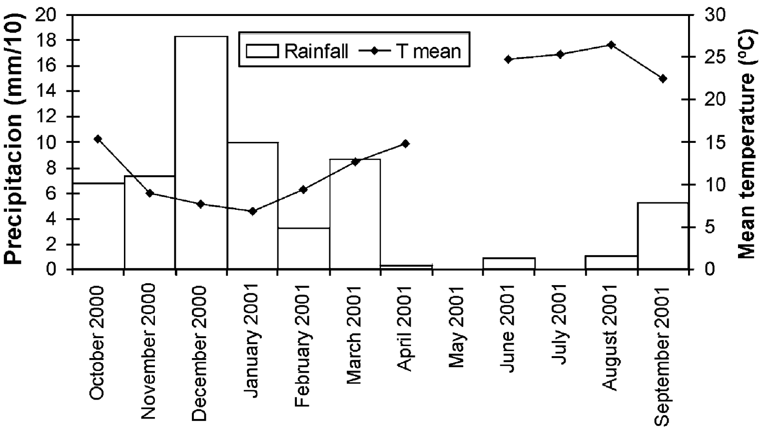

Fig. 1. Total rainfall (in mm/10; bars) and average temperature (in °C; line), by month from the Cubillas reservoir. No data were available for May.

nearby habitats that are moister (Moreno-Rueda, 2002). We might expect similar adaptive strategies to avoid dehydration in both species, but the two species have different world distributions and evolutionary origins. *S. candidissima* belongs to the family Sphincterochilidae, which is widespread around the Mediterranean basin, this species being distributed in the west of the basin (Alonso and Ibáñez, 1979; Fechter and Falkner, 1993). Species in this family are well adapted to subdesert environments (e.g. Yom-Tov, 1971a; Shachak, 1981; Steinberger et al., 1983; Arad et al., 1989). On the other hand, *I. gualtieranus* belongs to the family Helicidae, which is distributed throughout the western palaearctic (Fechter and Falkner, 1993). *I. gualtieranus* is endemic to Spain, and has a highly variable shell morphology, ranging from globose to flattened (López-Alcántara et al., 1985). All forms of this species live in Mediterranean habitats, but flattened forms (*I. g. gualtieranus*) dwell karstic sierras with drier climates (Alonso et al., 1985). This subspecies (see Elejalde et al., 2005) is the one studied here.

Because the two species have different evolutionary histories, they could have different adaptations, or different constraints, to inhabit dry habitats such as Sierra Elvira. For example, resistance to dehydration in the genera *Eremina* and *Euchondrus* is related to their different zoogeographic origins, with species from drier areas being more resistant to dehydration (Arad, 1993). Species less resistant to dehydration may be sheltered in protective microhabitat during critical drought periods to compensate for physiological or morphological deficiencies (Arad et al., 1989; Cook, 2001). In the present study, I analyse the seasonal use of refuges by both species in sympatry to understand the adaptive strategies that allows both species to dwell in dry environments.

2. Material and methods

The study was carried out from October 2000 to August 2001, in a 500 m^2 site on the Sierra Elvira (southern Spain; 37°14′N, 3°47′W) with the typical habitat of both species (Moreno-Rueda, 2002): rocky terrain with a southern orientation and scrubby plants, especially rosemary (*Rosmarinus officinalis*). Climate on the study area (average temperature and total precipitation by month) is presented in Fig. 1 (from the reservoir of Cubillas, four kilometres from the study area and at the same altitude, about 630 m als). The study area was divided in plots of 9 m^2. Sampling was performed around the 15th day of the month, with 1–7 days sampling per month (no data for May). I sampled 5 plots per day, and no plot was sampled more than once per month.

I considered snails as inactive when their bodies were secluded inside their shells with an epyphragm closing the entrance. In total, 95.9% ($n = 412$) of *S. candidissima* and 71.2% ($n = 243$) of *I. g. gualtieranus* were inactive. For each inactive snail I recorded the species, and whether it was immature or adult, immature snails lacking an apertural lip (Fechter and Falkner, 1993). I also recorded the nature of snail's microhabitat: in vegetation, under a stone or inside a crevice; or whether no refuge was used (i.e. the snail was exposed to sunlight). An individual was considered sheltered by a plant when found shaded under the canopy or on the stems or branches. The plan area covered by the plant, the canopy area, was calculated using the formula of an ellipse: $\pi \times$ (maximum width/2) $\times$ (perpendicular width/2). Stones were measured similarly. For crevices, measurements were taken of the maximum width of the entrance (Wc), the maximum length of the entrance (Lc), and the maximum depth of the crevice. The entrance area of the crevice was calculated as $(Lc \times Wc)/2$, assuming the morphology of a rhombus. I recorded the orientation faced by the surface where refuges were (north, west, south or east). I measured the orientation because it is predictable that the species less resistant against dehydration should avoid the hottest orientations.

The kinds of refuges available in the study area and their characteristics were recorded. For this, I selected six 9 m^2 plots representative of the whole area, according to my experience. In these plots, all stones, shrubs and crevices sufficiently large to shelter a snail were measured as described above. In the same plots, at 165 random points, I measured the orientation faced by refuge's surface in order to determinate the orientations available in the study area.

Data were grouped in seasons according to the Julian calendar (autumn, winter, spring and summer) because sample sizes were too low to a monthly analysis. Kolmogorov–Smirnov tests were used to ascertain whether the variables were normally distributed. Parametric statistics were used with normal or normalised variables, while non-parametric statistics were used with variables that could not be normalised (Siegel and Castellan, 1988; Sokal and Rohlf, 1995). Data are shown as percentages, number of observations or mean ± standard deviation.

3. Results

3.1. Density of individuals through seasons

The density of *Sphincsterochila candidissima* was higher in spring and summer than in autumn and winter (Kruskal–Wallis; $H_{3,150} = 66.04$; $P < 0.001$; Fig. 2). Higher densities were found in seasons when temperature was highest and rainfall was lowest (Fig. 1).

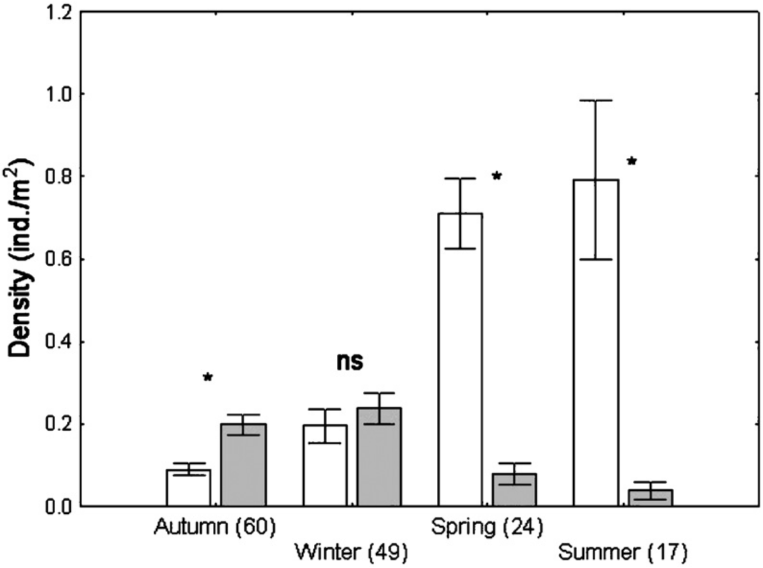

Fig. 2. Densities (individuals/m^2) of *S. candidissima* (white) and *I. g. gualtieranus* (grey) according to season. Bars show the standard error. Number of plots sampled is shown in parenthesis. Comparisons of average density performed with the Wilcoxon matched pairs test: $^*p < 0.001$; ns: not significant.

The lower densities during autumn and winter might be because the snails burrowed into the soil during those seasons. To test this, I performed some random prospecting in the soil, and 19 individuals were found burrowed in the humus under rosemary plants, at about one centimetre deep, in autumn and winter but not in spring or summer, although the sampling effort was similar. Density of *I. g. gualtieranus* also differed with seasons ($H_{3,150} = 22.60$; $p < 0.001$). However, density for this species was higher in autumn and winter, and lower in spring and summer (Fig. 1), the reverse of *S. candidissima. I. g. gualtieranus* was not found burrowed into the soil.

3.2. Selection of the type of refuge

For *I. g. gualtieranus*, immature individuals differed from adults in the sort of refuges they selected ($\chi^2_3 = 11.76$; $p < 0.01$; Table 1). Both immature and adult specimens were found sheltered mainly in crevices, but immatures used other types of refuges (bushes) more frequently than did adults (Table 1). Similarly, the frequencies of adult and immature individuals of *Sphincteroshila candidissima* in the refuges differed significantly ($\chi^2_3 = 15.11$; $p < 0.002$; Table 1). Because of these differences, adults and immatures were analysed separately in the comparisons between species.

Considering the whole year, significant differences existed among types of refuges used by *S. candidissima* and *I. g. gualtieranus* adults ($\chi^2_3 = 248.35$; $p < 0.001$; Table 1). 78% of *I. g. gualtieranus* were found in crevices, while only 7% of *S. candidissima* used this refuge (Fisher Exact Test, $p < 0.001$). In contrast, 46% of *S. candidissima* were sheltered in plants, versus 5% of *I. g. gualtieranus* (Fisher Exact Test, $p < 0.001$); and 47% of *S. candidissima*

Table 1
Numbers (percentages) of adult and immature *S. candidissima* and *I. gualtieranus* in the different types of refuges and according to season

	Sphincterochila candidissima				*Iberus g. gualtieranus*			
	Plant	Crevice	Stone	Unsheltered	Plant	Crevice	Stone	Unsheltered
Autumn								
Adult	16 (46)	8 (23)	0 (0)	11 (31)	3 (5)	37 (66)	4 (7)	12 (21)
Juvenile	3 (50)	2 (33)	0 (0)	1 (17)	1 (10)	8 (80)	0 (0)	1 (10)
Winter								
Adult	12 (26)	7 (15)	2 (4)	26 (55)	3 (6)	49 (91)	0 (0)	2 (4)
Juvenile	2 (12)	2 (12)	0 (0)	13 (76)	6 (26)	11 (48)	2 (9)	4 (17)
Spring								
Adult	43 (31)	4 (3)	0 (0)	90 (66)	0 (0)	8 (73)	1 (9)	2 (18)
Juvenile	3 (11)	3 (11)	3 (11)	18 (67)	1 (7)	8 (57)	2 (14)	3 (21)
Summer								
Adult	70 (77)	1 (1)	0 (0)	20 (22)	0 (0)	4 (100)	0 (0)	0 (0)
Juvenile	23 (66)	0 (0)	3 (9)	9 (26)	1 (100)	0 (0)	0 (0)	0 (0)
Total								
Adult	141 (45)	20 (6)	2 (1)	147 (47)	6 (5)	98 (78)	5 (4)	16 (13)
Juvenile	31 (36)	7 (8)	6 (7)	41 (48)	9 (19)	27 (56)	4 (8)	8 (17)
All	172 (44)	27 (7)	8 (2)	186 (47)	15 (9)	125 (74)	9 (7)	21 (17)

were found unsheltered, versus only 13% of *I. g. gualtieranus* (Fisher Exact Test, $p<0.001$). Both species seldom used stones as refuges (Table 1). Considering each season separately, the two species used different refuges in all seasons (for all seasons, $\chi^2_3>25.00$; $p<0.001$; Table 1). *I. g. gualtieranus* regularly used crevices as refuges during all seasons, and there were no significant differences among seasons in the refuges selected by this species ($\chi^2_9=15.16$; $p=0.09$; Table 1). By contrast, the type of refuge selected by *S. candidissima* differed according to season ($\chi^2_9=114.67$; $p<0.001$; Table 1). The frequency of unsheltered *S. candidissima* was higher in winter and spring, and lowest in summer (Table 1). In summer, most of unsheltered snails were found adhered to indented angles on rocks or stones, while in other seasons individuals were rarely found adhered to either substrate. The use of plants was greatest in summer (Table 1), when many *S. candidissima* were found adhered to the vertical stems of plants. Juvenile's refuges differed between the two species ($\chi^2_3=39.23$; $p<0.001$; Table 1), exhibiting the same trends as in adults, but the low sample size hindered more detailed analyses.

3.3. *The characteristics of selected refuges*

To analyse differences in the characteristics of refuges selected, I combined seasons into: autumn–winter and spring–summer, because the sample size was insufficient to analyse the data by individual seasons. Figs. 1 and 2 justified this grouping: during autumn and winter *I. g. gualtieranus* was active (unpublished data) while *S. candidissima* was underground (see above), and during spring and summer *S. candidissima* did not burrow and *I. g. gualtieranus* appeared to seek shelter in depth crevices.

3.3.1. *Crevices*

Characteristics of crevices selected by *I. gualtieranus* did not differ significantly between the two periods (autumn–winter and spring–summer) (Table 2). Adults selected deeper crevices than juveniles (Table 2). Within the plots used to calculate refuge availability there were 36 adequate crevices (sufficiently large to harbour a snail). These crevices were significantly smaller than those selected by *I. g. gualtieranus* in entrance width, depth and entrance area, but not in entrance height (Table 2). *S. candidissima* selected the largest crevices among those in the study area (Table 2). Crevices selected had significantly larger entrance area during the period of spring–summer than during autumn–winter, but differences were not statistically significant for other traits (Table 2). *I. g. gualtieranus* selected deeper crevices than did *S. candidissima* (Table 2).

3.3.2. *Plants*

Two-thirds of the *I. g. gualtieranus* that sheltered in plants used rosemary, the most abundant plant in the study area. Bushes selected had surface areas similar to those of a random sample (selected: $1468\pm944\,\mathrm{cm}^2$; random sample: $1699\pm2251\,\mathrm{cm}^2$; $t=0.32$; $p=0.75$; $n_1=10$ and $n_2=58$), but were higher (selected: 37 ± 15 cm; random: 27 ± 15 cm; $t=2.00$; $p<0.05$). Sample size was too low for more detailed comparisons. *S. candidissima* selected plants with greater heights (40 ± 14 vs. 27 ± 15 cm) and surface area (4430 ± 6043 vs. $1699\pm2251\,\mathrm{cm}^2$) than in the random sample ($t>3.0$; $p\leqslant0.001$; $n_1=123$, $n_2=58$). This pattern of selection did not vary over the seasons in *S. candidissima* (ANOVA; plant height: $F_{3,119}=0.23$; canopy surface: $F_{3,119}=2.16$; for both traits, $p>0.1$). Immature and adult *S. candidissima* did not differ in the characteristics of plants selected (for both traits,

Table 2
Characteristics of crevices selected by the snails

	Entrance height (cm)	Entrance width (cm)	Depth (cm)	Entrance area (cm^2)
Iberus gualtieranus gualtieranus				
Autumn–winter (99)	14.5±16.5	8.1±8.0	17.9±21.0	68.1±135.0
Spring–summer (14)	11.8±12.6	10.1±11.5	11.5±7.8	78.7±113.2
	ns	ns	ns	ns
Adults (90)	14.1±16.9	8.5±9.3	19.0 ± 21.4	71.6±143.0
Immature (23)	14.4±12.5	7.7±3.8	9.2 ± 7.8	60.8±77.7
	ns	ns	$p<0.05$	ns
Sphincterochila candidissima				
Autumn–winter (16)	13.3±11.8	6.3±3.8	9.1±9.0	41.7±45.1
Spring–summer (6)	22.5±14.6	14.5±14.6	12.3±5.1	110.9±76.6
	ns	ns	ns	$p<0.05$
Adults (17)	15.2±13.1	8.2±9.6	10.8±9.1	52.2±55.3
Immature (5)	17.6±13.7	9.6±4.8	9.1±9.0	89.0±81.4
	ns	ns	ns	ns
Total *I. gualtieranus*	14.4±15.6	8.3±8.5*	17.1±19.9*	69.4±1132.1*
Total *S. candidissima*	15.8±13.0	8.6±8.7*	10.0±8.2*	60.6±62.0*
	ns	ns	$p<0.05$	ns
Random sample (36)	12.6±13.0	3.7±2.0	6.6±4.3	25.8±36.6

Comparisons performed with the Mann–Whitney *U*-test, between age categories, between species, and between the total for each species and the random sample. "ns" indicates a non-significant result.

*Indicates significant differences with the random sample (last row) with $p<0.05$. Between bracket in the first column the sample size.

$t<1.3$; $p>0.2$; adults: $n = 106$; juvenile, $n = 17$). There were no differences between the two species for height or surface area (for both traits, $t<2.0$; $p>0.1$).

3.4. Selection of orientation

The two species did not differ between age classes in the orientation of refuges used ($\chi^2_3<7.0$; $p>0.05$; data not shown for simplicity). During autumn–winter, there were no significant differences between the two species ($\chi^2_3 = 3.28$; $p>0.3$), and orientation for both species did not differ significantly from the orientation of 165 points randomly selected (*I. g. gualtieranus*: $\chi^2_3 = 1.08$; $p = 0.78$; *S. candidissima*: $\chi^2_3 = 3.99$; $p>0.2$; Fig. 3). Given that the study area was oriented overall to the south, most of refuges were oriented to this direction. However, during spring–summer *I. g. gualtieranus* preferentially selected the western orientation and rejected the southern orientation, the latter being the hottest orientation ($\chi^2_3 = 12.42$; $p = 0.006$; Fig. 3). The orientation selected by *S. candidissima* did not differ from that expected by chance ($\chi^2_3 = 5.71$; $p>0.1$). Consequently, the orientation for the two species differed significantly in the spring–summer period ($\chi^2_2 = 7.96$; $p<0.02$; a degree of freedom was lost because neither individual was oriented to the north; Fig. 3). The orientation selected by *I. g. gualtieranus* differed between autumn–winter and spring–summer ($\chi^2_3 = 8.94$; $p = 0.02$), while that of *S. candidissima* did not ($\chi^2_3 = 4.25$; $p = 0.24$; Fig. 3).

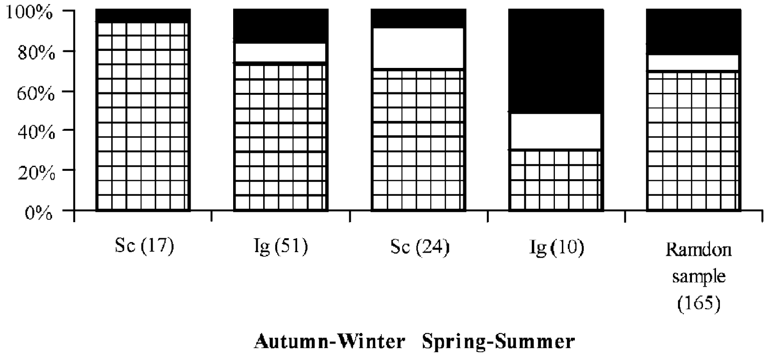

Fig. 3. Percentage of individuals found at different orientations during autumn–winter and spring–summer, and the percentage found in the random sample. Sc: *Sphincterochila candidissima*; Ig: *Iberus gualtieranus*. In parenthesis the sample size. Black: west; grey: north; white: east; squares: south.

4. Discussion

The results of this study show that the two species used different refuges available in the study area. The use of refuges and the cycle of both species may be divided in three periods:

(1) During autumn and winter, *S. candidissima* seemed burrowed into the humus under rosemary plants, probably to avoid the low temperatures of those seasons by hibernating, as the family Sphincterochilidae is from desert and subdesert zones (Fechter and Falkner, 1993), and *S. candidissima* may have a low tolerance to cold temperatures. It is improbable that they sought to avoid predators because predation by birds on this species is very rare (Yanes et al., 1991). While *S. candidissima* hibernated, *I. g. gualtieranus* remained active (unpublished) and did not hibernate in the year of the study.

(2) Spring appears to be the main activity period of *S. candidissima*, as most of them did not seek shelter. However, *I. g. gualtieranus* needed shelter during its activity period (autumn and winter; also see Moreno-Rueda, 2006) although that season is moister. *I. g. gualtieranus* started aestivation during spring, when *S. candidissima* was active. During aestivation, the density of *I. g. gualtieranus* was lower than during autumn and winter, probably because individuals were sheltered in the deepest crevices, where I could not find them.

(3) During summer, *S. candidissima* aestivated after climbing onto plants, the peristome adhering to the branches and stems. With this behaviour, the snails were exposed to sunlight, but at sites with higher air convection, and thus colder (Jaremovic and Rollo, 1979; Cowie, 1985; Slotow et al., 1993). In fact, individuals not found on plants were adhered to indented angles on rocks or stones, sites that probably also had higher air convection. Moreover, adhering to the substratum reduces exposure of the aperture to the environment, thereby reducing water losses (Luchtel and Deyrup-Olsen, 2001). *S. candidissima* individuals were not found buried in summer presumably because soil temperatures are very high (up to 70 °C registered during sampling; see also Cowie, 1985). This strategy of aestivation appears to be sufficient for the survival of

S. candidissima, whereas *I. g. gualtieranus*, for adequate shelter, aestivated deep inside crevices, presumably the best refuge in the study area. Moreover, during spring–summer, *I. g. gualtieranus* avoided sites with strong insolation (i.e. the south), while *S. candidissima* did not. *Theba pisana* also avoids the hottest orientations (Cowie, 1985).

In short, differences exist between the two species in the use of refuges that suggest that *I. gualtieranus* is more resistant to cold, while *S. candidissima* is more resistant to hot and drought. Morphology of the two species may account in fact for the differences in the use of microhabitats. *I. g. gualtieranus* has a flattened morphology (López-Alcántara et al., 1985), which evolved from *I. g. alonensis* (with globose morphology) probably as an adaptation to inhabit crevices in karstic and dry environments such as the Sierra Elvira (de Bartolomé, 1982; López-Alcántara et al., 1983; Elejalde et al., 2005). Indeed, Moreno-Rueda (unpublished manuscript) showed that individuals with more flattened shells had better access to crevices (in fact, *I. g. gualtieranus* had access to crevices deeper than those used by *S. candidissima*), and the present study shows that crevices are its primary refuge. This morphological adaptation seems improve the access to the only refuge (crevices) that gives adequate shelter against dehydration to this species, allowing it to survive in this habitat. Helicids seem to have a trend to evolve in this direction, given that other species of Mediterranean helicids have forms with flattened shells (de Bartolomé, 1982; Goodfriend, 1986; Mylonas et al., 1995).

While *I. g. gualtieranus* has evolved a morphology adapted to the use of a particular type of refuge (karstic crevices), *S. candidissima* has morphological features that probably make it more independent of refuges. (1) The shell of *S. candidissima* is pure white, while the shell of *I. g. gualtieranus* is pale brown (see, for example, Fechter and Falkner, 1993). Whiter shells reflect heat and thereby presumably reduce dehydration (Cameron, 1970; Yom-Tov, 1971b; Heath, 1975). (2) The shell of *S. candidissima* is also thicker than that of *I. g. gualtieranus* (pers. obs.), perhaps reducing water losses through the shell wall (Bar, 1978). (3) The aperture of *S. candidissima* is more reduced with respect to the total size of the shell than that of *I. g. gualtieranus* (pers. obs.), this also reducing water loss by transpiration (Cameron, 1981; Luchtel and Deyrup-Olsen, 2001). (4) While *I. g. gualtieranus* has a membranous epiphragm (pers. obs.), *S. candidissima* has a thick, calcic one, which would protect against water losses (Arad et al., 1989; Luchtel and Deyrup-Olsen, 2001). A morphology better adapted to arid environments may explain the wider distribution of this species.

Differences between immature and adult snails might imply that the smaller size of young snails makes them more versatile in refuge selection (e.g. Mylonas et al., 1995). On the other hand, smaller individuals have less capacity for movement, possibly limiting their availability to search for suitable refuges and thereby compelling them to select suboptimal refuges (Cowie, 1985).

Overall, this study suggests that these two species are the dominant species in the Sierra Elvira thanks to different adaptive strategies, which have evolved as a consequence of different morphological and physiological adaptations related to their different zoogeographic origins. *S. candidissima* seems better adapted to the dry habitat of the Sierra Elvira. Despite these differences, *I. g. gualtieranus* coexists in sympatry with *S. candidissima* at high densities. Instead of developing only physical adaptations against dehydration, *I. g. gualtieranus* uses a behavioural adaptation exploiting a highly protective refuge: karstic crevices, a behaviour that fuels the subsequent evolution of its flattened shell (López-Alcántara et al., 1983). Thus, behavioural adaptations may compensate for morphological and physiological deficiencies allowing land-snails to dwell in arid environments (Wcislo, 1989).

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