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Short Communication A

RELATIVE IMPORTANCE OF HUMIDITY AND TEMPERATURE ON MICROHABITAT USE BY LAND SNAILS IN ARID VERSUS HUMID ENVIRONMENTS

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ABSTRACT

Dry environments, characterized by high temperatures and low humidity, impose restrictive living conditions on animals, which are especially critical for hydrophilic animals such as terrestrial gastropods. In order to successfully inhabit arid zones, snails show a suite of adaptations, such as the selection of microhabitats to minimize dehydration risk. When dehydration risk is high, protective microhabitats should be selected, and therefore, microhabitat selection should be regulated by weather conditions. Moreover, the weather factor more restrictive for snail life (humidity or temperature) should be the primary one regulating microhabitat selection. Here, we analyze this with two sympatric arid-dwelling snails from southeastern Spain, *Iberus gualtieranus* and *Sphincterochila candidissima*, and compare the results with two other sympatric land-snails, *Theba pisana* and *Otala lactea*, from a humid Mediterranean zone. For the four

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snails, microhabitat use is affected by weather, but differences occurred between sites. In humid environments, only temperature regulates microhabitat selection by *T. pisana* and *O. lactea*, and these snails climb to vegetation when temperature is high in order to escape from heat shocks. Meanwhile, in arid environments, humidity is also an important variable regulating snail behavior, especially for *I. gualtieranus,* which is sheltered in karstic fissures when humidity is low. In contrast to this species, *S. candidissima* prefers to climb to vegetation to escape from dehydration. In sum, snails respond to adverse weather conditions selecting the most protective microhabitats, although the response varies with climatic conditions and among species.

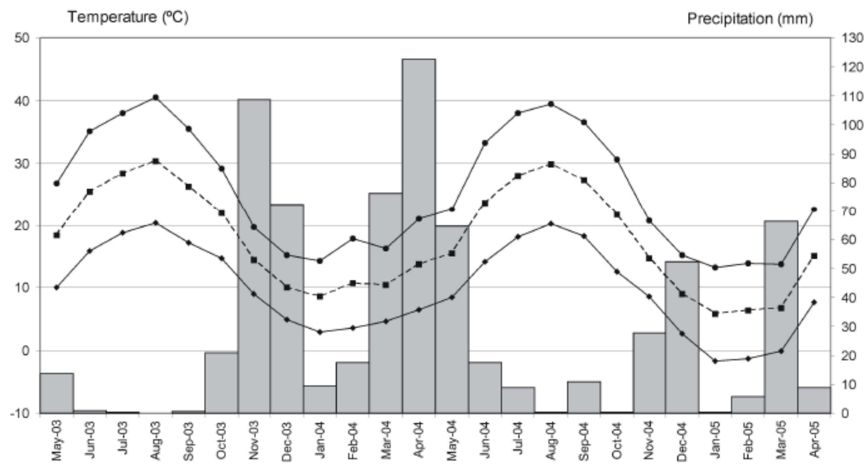
INTRODUCTION

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). For this reason, arid environments are very restrictive to gastropods. In fact, more species and individuals of terrestrial gastropods are found in moister zones (Tattersfield, 1990; Wardhaugh, 1995; Ports, 1996). Nevertheless, some snails dwell in arid zones thanks to a set of adaptations against dehydration. One such adaptation is the use of efficient microhabitats where the risk of dehydration is lower (Cook, 2001). For example, the land snail *Sphincterochila prophetarum* shelters itself under stones when moisture is lowest (Steinberger *et al.*, 1983), while *Cepaea nemoralis* climbs to vegetation, where temperature is lower, in order to escape from heat at the ground (Jaremovic and Rollo, 1979). However, land-snails in arid environments would need to leave protective microhabitats in order to find resources such as food and mates, if these resources can not be found in the protective microhabitats (Moreno-Rueda, 2006). Weather conditions should determine the correct time when land-snails may venture out of protective microhabitats, and only when weather conditions are less harmful for snails may these move onto less protective microhabitats against dehydration (Cook, 2001).

In the present chapter, we analyze how the weather regulates the use of microhabitats in four land-snails: *Sphincterochila candidissima*, *Iberus gualtieranus*, *Theba pisana* and *Otala lactea*. Snails should use less protective microhabitats when weather conditions are benign (i.e., wet), and stay in more protective microhabitats when weather conditions are harmful (dry). We also predict that the importance of weather on the microhabitat use is higher in arid environments, where the correct selection of microhabitat, at the right moment, is more important for survival. In order to test this, we studied the influence of weather (temperature and humidity) on the microhabitat use by these four species of Mediterranean land-snails in two zones with different climatic conditions: Sierra Elvira, an arid environment very restrictive for land-snails (*S. candidissima* and *I. gualtieranus*) (see Moreno-Rueda, 2002), and Barbate, a moisture coastal zone of southern Spain, representing an optimal environment for the activity of snail species (*T. pisana* and *O. lactea*).

STUDY AREAS

Sierra Elvira (Southeastern Spain; 37º 15' N, 3º 40' W) is a small karstic mountain with an altitudinal range of 600-1100 m a.s.l. The climate is mesomediterranean accentuated (UNESCO, 1963; Rivas Martínez, 1987). Annual precipitation is less than 500 mm, with five months of drought (Alonso *et al*., 1985; figure 1). Therefore, it is a harsh environment for hydrophilic animals such as gastropods. Habitat in the study zone is rocky substrates with karstic erosion and low vegetal cover, conformed mainly by rosemary (*Rosmarinus officinalis*) and grass.



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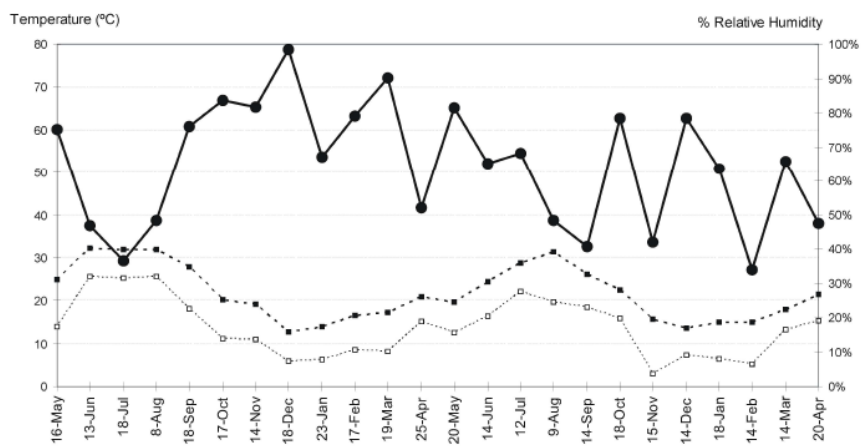

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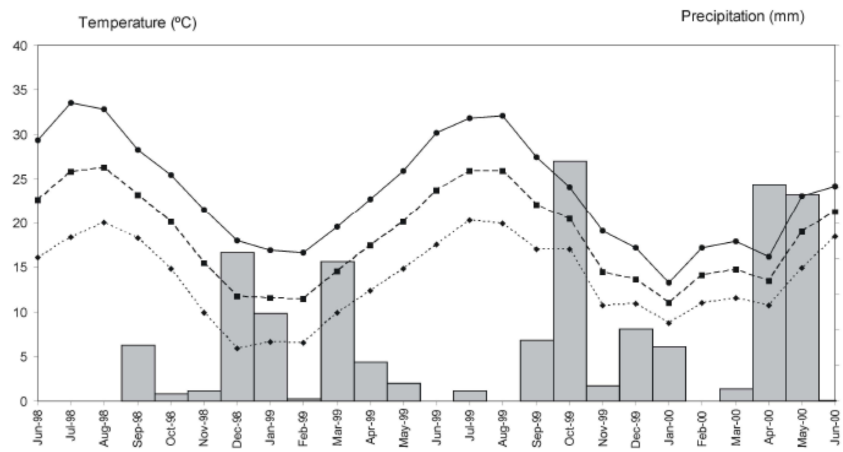
Figure 1. A) Weather of Sierra Elvira, according to the meteorological station of Pinos Puente. For each month it is showed precipitation (bars), maximal mean temperature (circles and upper continuous line), average temperature (squares and dashed line) and minimal mean temperature (rhombuses and lower continuous line). B) Weather variables measured *in situ* during the sampling: relative humidity (circles), temperature at the level of ground (fill squares) and temperature at 5-cm on ground (open squares).

Barbate (Southern Spain, 36º 11’ N, 5º 55’ W) is located in a recent mixed alluvial-estuarine marsh (“Marismas del río Barbate”), that keeps most of its natural dynamics and has a high productivity. The climate is oceanic Mediterranean, with a period of summer relatively drought (two-three months, from June to August; figure 2), mean annual rainfall of 880 mm (though largely variable), mean annual temperature of 14.6 ºC, and mean annual relative humidity close to 80% (Consejería de Medio Ambiente, 2000).



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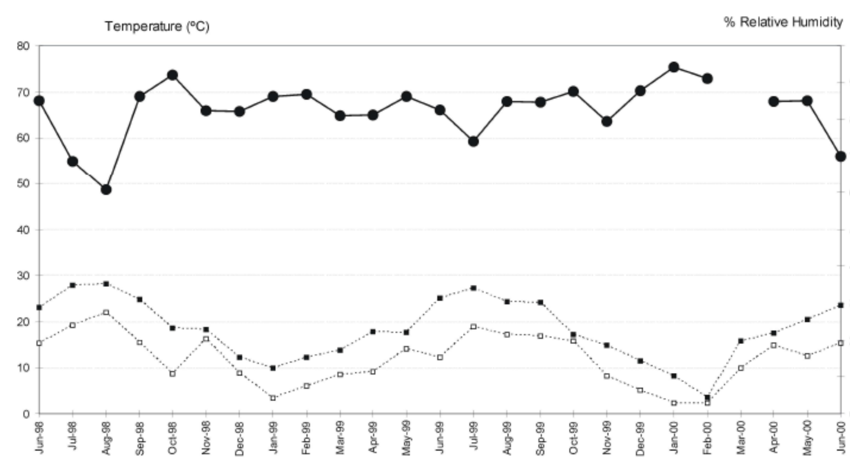

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Figure 2. A) Weather of Barbate, according to the meteorological station of Vejer. For each month is shown precipitation (bars), maximal mean temperature (circles and upper continuous line), average temperature (squares and dashed line) and minimal mean temperature (rhombuses and lower continuous line). B) Weather variables measured in situ during the sampling: relative humidity (circles), temperature at the level of ground (fill squares) and temperature at 5-cm on ground (open squares).

Considering the data measured *in situ*, there was no difference between Sierra Elvira and Barbate in temperature at ground level, nor 5 cm above ground (Student *t*-test, $t_{46} < 1.6$; $p > 0.10$; see figures 1b and 2b). However, relative humidity measured during sampling was significantly higher in Barbate than in Sierra Elvira ($t_{46} = 4.81$; $p < 0.001$; figures 1b and 2b). Therefore, while temperature was similar in both zones, humidity was significantly lower in

Sierra Elvira. Temperature was significantly higher at ground level than at 5 cm above ground, so in Sierra Elvira as in Barbate (in both cases, paired *t*-test, $t_{23\text{-}62} > 18.0$; $p < 0.001$; figures 1b and 2b).

STUDY SPECIES

Sphincterochila candidissima (Draparnaud, 1801) is a Mediterranean arid-dwelling land-snail (Fechner and Falkner, 1993), which exhibits several adaptations typical of desert snails against dehydration, such as thick shell, small aperture, and white color (Moreno-Rueda, 2002, 2007, 2008). This snail is active only during four months in Sierra Elvira, during spring and autumn, while during winter it is buried under humus, and during summer it climbs to vegetation presumably in order to escape from heat, which is usually higher at the bottom (Moreno-Rueda, 2007; Moreno-Rueda and Collantes-Martín, 2007). For this snail, therefore, the protective microhabitat in summer is vegetation, and it should be found on vegetation when weather is drier.

We also studied in Sierra Elvira the land-snail *Iberus gualtieranus* (Linnaeus, 1758), concretely the subspecies *I. g. gualtieranus* (Elejalde et al., 2005, 2008). This subspecies is an arid-dwelling snail suited to arid and karstic environments (Alonso et al., 1985), but it does not exhibit typical morphological adaptations against dehydration of desert snails (as *S. candidissima* does; Moreno-Rueda, 2002, 2007). It is not white, but pale brown; and its aperture is relatively big. *Iberus gualtieranus* dwells in arid environments such as Sierra Elvira thanks to the use of very protective refuges against dehydration, the karstic crevices, where a fresh and moisture microclimate remains (Moreno-Rueda, 2007). However, food resources of this snail are on bare soil, which obligates it to move out of these protective microhabitats in rocky substrate (Moreno-Rueda, 2006). Accordingly, *I. gualtieranus* should be found on rock (protective microhabitat) when weather is dry, and on bare soil (no protective microhabitat), when it is benign. Moreover, during summer, the detected density of this snail decreases, as individuals are deeper in the karstic fissures, escaping from heat (Moreno-Rueda, 2007). For this reason, we also expect that weather should affect the density of individuals of this species detected at the surface.

Theba pisana (Müller, 1774) is a typical Mediterranean land-snail that does not inhabit the Sierra Elvira. In Barbate, a milder zone with high humidity (see above), this species shows activity during the complete year, although the percentage of active individuals is lower during summer months (unpublished data). When heat is high, this snail climbs to vegetation, where temperature is lower (Cowie, 1985; this chapter).

Otala lactea (Müller, 1774) is also a Mediterranean land-snail that does not inhabit environments as harsh as Sierra Elvira. In Barbate, this species, as *T. pisana*, usually shows activity during practically the complete year, although the frequency of active individuals is also lower during summer months (unpublished data). This snail is found on vegetation and on bare soil substrates. If, as other species (Jaremovic and Rollo, 1979; Cowie, 1985; Slotow et al., 1993), *O. lactea* climbs to vegetation to escape from heat, we expect that weather modulates its behavior on microhabitat selection.

SAMPLING METHOD

The study plot for *Otala lactea* and *Theba pisana* in Barbate had an area of 392 m^2 (14 × 28 m), while in Sierra Elvira we used a plot of 120 m^2 (20 × 6 m) for *Sphincterochila candidissima*, and other adjacent of 280 m^2 (20 × 14 m) for *Iberus gualtieranus*. The plots were divided into 4-m^2 squares (2 × 2 m). The study areas were visited each month. Barbate was visited from June 1998 to August 2000 (*n* = 23 months for *O. lactea*; *n* = 22 months for *T. pisana*), and Sierra Elvira was visited from May 2003 to May 2004 (*n* = 13 months for *I. gualtieranus*; *n* = 12 months for *S. candidissima*). The fieldwork started between 23:00 and 24:00 hours. We surveyed the study plot for about 4 hours, with a single observer for each species (always the same), applying a total of 4 minutes of searching in each 4-m^2 square. For each individual snail found, we registered maturity (adults, those with reflected and thickened peristome, or juveniles), substrate position (on bare soil, on rock, on vegetation, or other substrate such as waste), and the state (either dormant -with epiphragm, or active -without epiphragm).

In each survey we registered the air (5 cm above ground) and soil temperatures and the air relative humidity at 1-hour intervals. Furthermore, we obtained meteorological data (temperature and rainfall) from the meteorological station in Vejer (National Meteorology Institute of Spain), about 7 km away of Barbate, for the sampling period. We also obtained information from the meteorological station in Pinos Puente, close to the Sierra Elvira plots. Meteorological data consisted of temperature mean, maximal and minimal, and precipitation.

STATISTICAL ANALYSES

All variables were normally distributed according to a Kolmogorov-Smirnov test, and parametric statistics were used. A Principal Components Analysis (PCA) showed that, in Sierra Elvira, all variables of temperature were strongly correlated in between, and weather variables related to humidity were strongly correlated in between. In order to diminish the number of variables used, we extracted a PCA factor for all variables of temperature, named "Temperature index", and other factor for variables of humidity and precipitation named "Humidity index". For Barbate, we only used the variables of temperature and relative humidity obtained *in situ* (figure 2b), because previous unpublished results showed, for this locality, differences in snail behavior in close sites due to differences in microclimatic conditions.

We first examined the correlations among weather variables (humidity and temperature) and the frequency (transformed by the arc-sin of squared root; Sokal and Rohlf, 1995) of individuals of each species on each substrate type (rock, bare soil or vegetation in Sierra Elvira; bare soil or vegetation in Barbate—rock is very improbable here). Afterwards, in order to know the direct effect of each variable, statistically controlled for the effect of the other predictor variable, we calculated partial correlations (see Sokal and Rohlf, 1995), by performing a multiple regression with specimen frequency in each substrate as dependent variable, and humidity and temperature variables as independent predictors. Data are showed as mean ± standard deviation.

RESULTS

Sphincterochila candidissima in Sierra Elvira

Throughout the complete year of the study, most of the *Sphincterochila candidissima* snails were found on bare soil (55.7 ± 8.9%), with a lower percentage found on rock (22.0 ± 5.6%) and vegetation (22.3 ± 6.8%) (see figure 3). There was no effect of weather (temperature and humidity indexes) on the percentage of individuals found on rocky substrate (p > 0.15). However, the percentage of individuals found on plant substrate increased with temperature (r = 0.75; p = 0.005) and decreased with humidity (r = -0.68; p = 0.015). In contrast, when the temperature was the lowest (r = -0.78; p < 0.01) and humidity was higher (r = 0.72; p < 0.01), more specimens were found on bare soil, their main substrate.

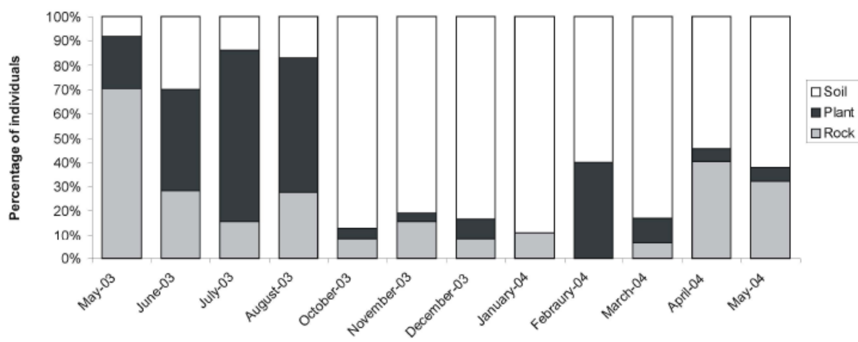

Figure 3. Frequency of *Sphincterochila candidissima* in each type of substratum during each sampled month in Sierra Elvira. White: bare soil; black: vegetation; grey: rock.

As temperature and humidity are correlated in Sierra Elvira (r = -0.76; p = 0.005), we performed multiple regression analyses in order to test the independent effect of the two weather factors on the substrate selected by *S. candidissima*. Tolerance between temperature and humidity was 0.43, higher than 0.30, and therefore suggesting that multicollineratity was not a problem (Quinn and Keough, 2002). Whole models for the use of bare soil ($F_{2, 9}$ = 8.34; p < 0.001; R^2 = 0.65) and plant ($F_{2, 9}$ = 6.63; p < 0.02; R^2 = 0.60) were significant and explained 60-65% of variation in the use of these substrates. However, the independent effect of humidity and temperature was not significant in the models (always p > 0.10 for partial correlations). In conclusion, we failed in separate the independent effects of humidity and temperature on substrate selection in *S. candidissima*.

Iberus gualtieranus in Sierra Elvira

For *Iberus gualtieranus,* the main substrate was rock (86.0 ± 3.4%), and they rarely used bare soil (7.2 ± 2.3%) or plants (6.9 ± 1.9%) (see figure 4). The percentage of individuals found on bare soil strongly increased with humidity (r = 0.80; p = 0.002), but was not significantly correlated with temperature (r = -0.50; p = 0.10). In a model of multiple regression, only humidity significantly affected the percentage of individuals found on bare soil ($F_{2, 9}$ = 9.16; p < 0.01; R^2 = 0.67; partial correlation for humidity $r_{partial}$ = 0.75; p < 0.01; for temperature: $r_{partial}$ = 0.27; p = 0.42). On the other hand, there was no significant correlation among temperature or humidity and the percentage of individuals found on rocks and plants (always p > 0.05). Therefore, it seems that humidity mediates the use of substrates by *I. gualtieranus*, and this snail is on bare soil most frequently when humidity is high. Lastly, the abundance of *I. gualtieranus* was significantly mediated by temperature (r = -0.63; p < 0.05; figure 5), but not significantly by humidity (r = 0.50; p = 0.10).

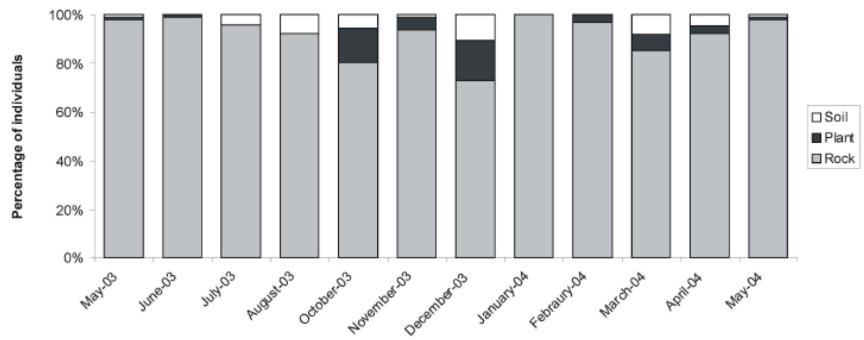

Figure 4. Frequency of *Iberus gualtieranus* in each type of substratum during each sampled month in Sierra Elvira. White: bare soil; black: vegetation; grey: rock.

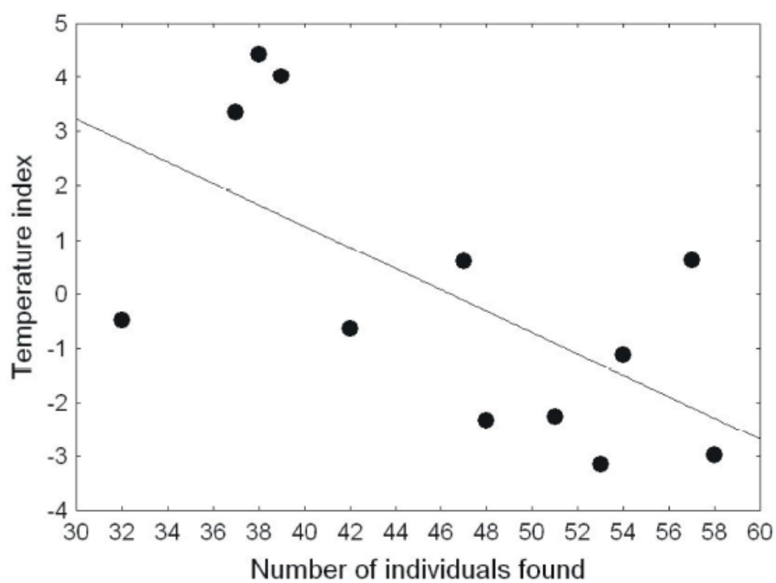

Figure 5. Relationship between temperature index and density of *I. gualtieranus* individuals in Sierra Elvira.

Theba pisana in Barbate

The 87.4 ± 3.6 % of *Theba pisana* individuals in Barbate were found on plants, versus 8.7 ± 3.6 % found on bare soil (the rest were found on other diverse substrates) (figure 6). The frequency of individuals on plants increased with soil temperature (r = 0.76; p < 0.001), but showed no significant variation with humidity (r = 0.03; p = 0.91). The frequency of individuals on bare soil decreased with temperature (r = -0.62; p = 0.02), and was not significantly related to humidity (r = -0.19; p = 0.40). In Barbate, soil humidity and temperature were not significantly correlated (r = -0.22; p = 0.33; n = 22). In spite of this, we performed models of multiple regressions which confirmed the previous results by the simple correlations. The frequency of individuals on bare soil was determined by soil temperature ($F_{2,\ 19}$ = 9.34; p = 0.001; R^2 = 0.50; partial correlation for temperature $r_{partial}$ = -0.69; p < 0.001; for humidity, $r_{partial}$ = -0.42; p = 0.06). Evenly, the frequency of individuals on plants was determined only by soil temperature ($F_{2,\ 19}$ = 15.63; p < 0.001; R^2 = 0.62; partial correlation for temperature $r_{partial}$ = 0.79; p < 0.001; for humidity, $r_{partial}$ = 0.31; p = 0.18). Tolerance between humidity and temperature in the models was 0.95. In conclusion, only soil temperature determined substrate use by this land-snail.

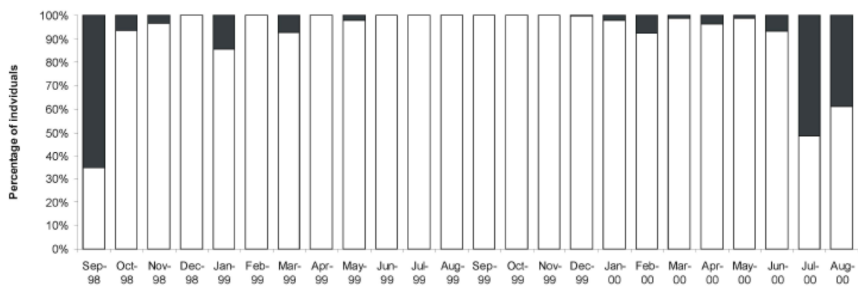

Figure 6. Frequency of *Theba pisana* in each type of substratum during each sampled month in Barbate. White: vegetation; black: bare soil.

Otala lactea in Barbate

More specimens of this species were on plants (60 ± 3.2 %) than on bare soil (19.6 ± 3.2 %; figure 7). For *Otala lactea*, there was a negative non-significant correlation between soil temperature and frequency of individuals on bare soil (r = -0.40; p = 0.06; n = 23 months). This correlation become significant when statistically controlling for the effect of humidity (partial correlation $r_{partial}$ = -0.46; p < 0.05). The correlation among weather variables (temperature at the level of soil and relative humidity) and the frequency of individuals on plants, and the correlation between humidity and individuals on bare soil were not significant (always p > 0.50; n = 23).

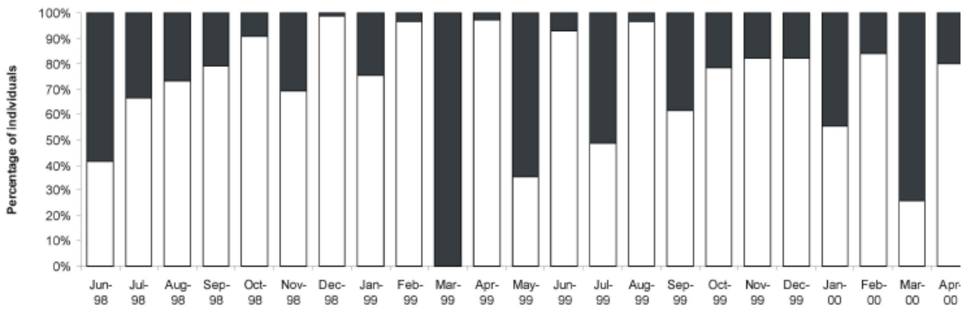

Figure 7. Frequency of *Otala lactea* in each type of substratum during each sampled month in Barbate. White: vegetation; black: bare soil.

CONCLUSION

Results in this chapter show that land-snails select microhabitat according to weather conditions, being found primarily on microhabitats protective against dehydration when humidity is low and/or temperature is high. However, the relative importance of humidity determining microhabitat selection was higher in Sierra Elvira, an arid zone, than in Barbate, a zone with higher environmental humidity. In Barbate, temperature was the only factor that statistically affected microhabitat selection by *Theba pisana* and *Otala lactea*. In Sierra Elvira, in return, temperature as well as humidity affected microhabitat selection by *Sphincterochila candidissima*, while for *Iberus gualtieranus* humidity was the primary factor affecting snail behavior. As explained, in Barbate humidity is high during almost the complete year, and for this reason it is not a determinant factor on snail behavior. In contrast, temperature affects dehydration risk of individuals and become an important factor regulating microhabitat selection. In an arid zone as Sierra Elvira, the low level of environmental humidity is a primary factor for the survival of snails, being an important variable affecting the behavior of microhabitat selection, even more important than temperature for *I. gualtieranus*.

Sphincterochila candidissima, *T. pisana* and *O. lactea* climbed to vegetation when temperature was adverse (very high), while more frequency of individuals were found on bare soil when conditions were benign. On plants, these snails are exposed to a lower temperature than on the ground, decreasing the risk of dehydration (Jaremovic and Rollo, 1979; Cowie, 1985; Moreno-Rueda and Collantes-Martín, 2007). In the present study, as found in other studies, temperature was significantly lower 5 cm above ground than directly on the ground in Sierra Elvira and Barbate. Therefore, it is clear that by climbing on plants, snails find a cooler microclimate than on the ground. This probably increases their survival in conditions of stress provoked by adverse weather.

Iberus gualtieranus, in return, shelters in fissures in rocks, although it is active on bare soil (Moreno-Rueda, 2006). Activity of this land-snail is determined primarily by humidity, with more specimens active when humidity is higher (unpublished data). This should cause more individuals to be on bare soil when humidity is higher, and effectively, the frequency of individuals found on bare soil increased with the percentage of active snails (r = 0.78; p = 0.003; n = 12 months). On the other hand, the higher the temperature, the lower the frequency of individuals found on the surface, probably because individuals were deeper in rocky crevices, escaping from heat at the surface (Moreno-Rueda, 2007). This species, thus, showed a strategy to avoid dehydration different from the other ones (*S. candidissima, T. pisana* and *O. lactea*). While the strategy of climbing to vegetation seems to be generalized among snails, the use of rocky crevices is less common. Probably, climbing to vegetation would be insufficient for survival in *I. gualtieranus*, which is obligated to use less accessible refuges (which has fueled the evolution of a flattened shell; López-Alcántara *et al*., 1983), while for the sympatric *S. candidissima* probably this strategy is sufficient for survival in Sierra Elvira, thanks to other adaptations against dehydration (see Moreno-Rueda, 2007).

Currently, the Earth is under a global warming (IPCC, 2001), which may contribute to the extinction of several species (Thomas *et al*., 2004). Land-snails, being very sensitive to environmental conditions of weather, may be especially prone to extinction as a consequence of this warming. In fact, the extinction of some populations has been related to climatic change (Baur and Baur, 1993; Gerlach, 2007). Two of the species studied here, *T. pisana* and *O. lactea*, are important as commercial food resources (Arrébola *et al*., 2004a, b). *Iberus g. gualtieranus*, moreover, is also an endangered taxon (Arrébola and Ruiz-Ruiz, 2006). Survival capacity of populations faced with climatic change will depend, in part, on the plastic capacity of individuals to become adapted to the new climatic conditions. Results in the present chapter suggest that snails have certain capacity of response to a rise of temperature, by selecting the adequate microhabitat in each moment in order to survive. This degree of response capacity may help in the survival of some populations, while there are microhabitats available.

In conclusion, the results in this study show that snails may respond to adverse weather conditions by selecting the adequate microhabitat at each moment. Climbing to vegetation is a generalized strategy, although, especially in arid zones, it may be insufficient for the survival of some species. Furthermore, the importance of different weather variables (temperature versus humidity) on the use of microhabitat varies geographically, humidity being more important than temperature in arid zones.

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